Vol. XIV, No. 4 November, 1927

THE ANNALS OF APPLIED BIOLOGY

EDITED FOR THE ASSOCIATION OF ECONOMIC BIOLOGISTS

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BOMBAY, CALCUTTA, MADRAS: MACMILLAN & CO., LTD.
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PRINTED IN GREAT BRITAIN

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COMPARISON BETWEEN KAURI PINE AND SWAMP KAURI (*AGATHIS AUSTRALIS*)

BY J. F. MARTLEY, A.R.C.S., M.Sc.
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OWING to the decreasing supplies of kauri pine the market has had recourse to the supplies of swamp kauri in order to keep pace with the demand for this valuable New Zealand timber.

Swamp kauri is the name given in the trade to the timber milled from the buried logs of kauri pines (*Agathis australis*) which flourished in the distant past and which have been preserved to the present day by being submerged in their native swamps. The high price of kauri pine has made the extraction and utilisation of these logs a remunerative business, especially as it is difficult to distinguish with any degree of certainty between swamp kauri and kauri derived from trees grown in the present time.

As users of kauri pine are doubtful whether the qualities of swamp kauri approach the excellence of those of kauri pine it has been necessary to examine a number of specimens in order to find if it is possible to distinguish the timber derived from felled logs from that obtained from the submerged logs.

The material for examination consisted of some ten reputed samples of various sizes of kauri pine, and of four samples of reputed swamp kauri which had been obtained by the Forest Products Research Laboratory through the courtesy of various London firms. All the samples had been air dried and several of the specimens had been in storage for a considerable number of years. Unfortunately no determinations were made of the moisture content of the samples when they were received, but probably none had a moisture content in excess of about 25 per cent.

Comparisons between swamp and normal kauri were confined to an examination for structural differences observable under the microscope, to the measurement of the amount of swelling and shrinking ("working") with change of moisture content, and to the determination of the moisture content when in equilibrium with an atmosphere of a given

relative humidity and of the density of the wood substance composing the different samples.

In the microscopic examination no consistent difference could be found between the normal and the swamp kauri. In both the number of resin tracheids was substantially the same. The only difference that could be noted was that the number of tracheids with inclined striae on their walls was slightly greater in the swamp material than in the normal though in neither case were these markings either numerous or pronounced.

Table I.

Kauri pine. Data on the shrinkage of five specimens derived from two samples of kauri pine on being oven dried at 105° *C.*

	Kauri 1		Kauri 2		
	a	*b*	*a*	*b*	*c*
Weight in gm.	16·994	16·415	25·074	27·823	29·751
Volume in cm.³	29·31	28·39	40·23	43·50	48·48
Density	·580	·578	·623	·640	·614
% moisture content	14·09	14·13	10·89	11·22	11·07
Oven dry weight	14·896	14·383	22·616	25·016	27·787
Oven dry volume	27·29	26·39	38·68	42·21	46·90
Oven dry density	·546	·545	·585	·593	·571
Moisture loss in gm.	2·098	2·032	2·458	2·807	2·964
Volume loss in cm.³	2·02	2·00	1·55	1·39	1·58
Volume change per loss of 1 gm. moisture	·963	·984	·631	·495	·506

Table II.

Swamp kauri. Data on the shrinkage of six specimens, three from each of two samples of swamp kauri, on being oven dried at 105° *C.*

	Swamp kauri 1			Swamp kauri 2		
	a	*b*	*c*	*a*	*b*	*c*
Weight in gm.	31·465	32·650	31·490	54·980	53·208	53·392
Volume in cm.³	53·59	54·76	52·50	89·91	87·78	89·13
Density	·587	·596	·600	·615	·606	·598
% moisture content	13·82	13·71	13·35	13·05	12·86	12·65
Oven dry weight	27·645	28·712	27·782	48·634	47·144	47·396
Oven dry volume	51·57	52·94	50·78	86·20	85·94	86·40
Oven dry density	·536	·542	·547	·564	·549	·549
Moisture loss in gm.	3·820	3·938	3·708	6·346	6·064	5·996
Volume loss in cm.³	2·02	1·82	1·72	3·71	1·84	2·73
Volume change per loss of 1 gm. moisture	·529	·462	·464	·585	·303	·455

The comparisons of the changes in volume which occurred in the two types of material on change of moisture content were made by measuring the volume of a number of rectangular blocks of about 50 cm.^{3} in size, in the air dry state under current laboratory conditions and again after drying in an oven at 105° C.

Two samples of normal kauri were taken and two of swamp kauri and measurements were made, except in one case, of the dimensions of three rectangular blocks prepared from each of the four samples. Each dimension of a block was taken as the mean of the measurements made at nine different points with a screw gauge measuring to 1/50 mm. The results of the measurements made before and after drying are given in Tables I and II, in the last line of which will be found the shrinkage in volume that the blocks suffered on losing one gramme of moisture.

It is seen from the figures that although there is a certain amount of overlapping among the figures, the shrinkage of swamp kauri is definitely less than that of normal wood losing moisture under the same conditions. Although the shrinkage was measured over a different range of moisture content, this result is in agreement with the finding of Janka(1) that wood which had been soaked for a period of one and a half to three years in salt or in fresh water shrank less on drying from the wet to the air dry condition than green wood which had not been so treated.

The hygroscopicity measurements were made by suspending a slip of wood, 0·50 mm. thick and weighing about 0·10 gm. from a calibrated spring supported in a glass vessel made by cementing together pieces of sheet glass of suitable size. The relative humidity in a vessel was kept at a constant value by the presence of some suitable salt moistened with water. The extension of the spring was measured with a travelling microscope reading to 1/50th mm., when the wood had reached the moisture content in equilibrium with the atmosphere in the vessel. From the oven dry weight of the slip of wood which was determined subsequently, and the spring calibration chart it was a simple matter to calculate the moisture content in the different relative humidities. The sensitivity of the springs used was such that with a load of about 0·10 gm. an extension of 1/50th mm. was equivalent to a difference in moisture content of somewhat less than 0·04 per cent.

The following salts were used to condition the air within the vessels: sodium chloride and the hexahydrate of calcium chloride in the presence of a small quantity of water, and fused calcium chloride. The relative humidities over these salts at laboratory temperatures are approximately 75, 35 and 3 per cent. respectively—Obermiller(2).

The spring extension was found for each of the two specimens of normal kauri pine and swamp kauri in the successive relative humidities of the following cycle: 75, 35, 3, 35 and 75 per cent., by transferring the specimen while still suspended from its spring to the next vessel after equilibrium had been reached in the previous atmosphere.

Table III.

Comparison of the equilibrium moisture content of two specimens each of kauri pine and of swamp kauri over the given relative humidity cycle. Temperatures at the time of equilibrium given in each case.

Salt	Approximate relative humidity %	Kauri pine				Swamp kauri			
		No. 2		No. 3		No. 2		No. 3	
		% M.C.	°C.	% M.C.	°C.	% M.C.	°C.	% M.C.	°C.
1. NaCl	75	15·0	13	15·7	12	16·3	16	15·9	16
2. $CaCl_2$, $6H_2O$	35	11·4	11	11·9	12	12·1	16	11·0	17
3. $CaCl_2$	3	6·4	12	6·6	15	4·3	17	2·6	17
4. $CaCl_2$, $6H_2O$	35	9·9	13	10·1	18	9·8	15	9·4	17
5. NaCl	75	15·1	13	15·7	16	16·0	13	15·8	17

The moisture contents of the samples of normal and swamp kauri in the successive stages of the above relative humidity cycle are given in Table III. No attempt was made to keep the temperature constant, but in the table the temperature of the air close to the vessel is given at the time of measurement of the spring extension. On the analogy with the effect of temperature on the regain of cotton and other materials, Wilson and Fuwa (6), the temperature effect in these experiments will be less than the experimental variation.

It will be seen from the figures in the table that there is no constant difference between the normal and the swamp kauri as far as regards hygroscopicity. The reason for the considerable differences in the moisture content of the samples in the atmosphere controlled by "dry" calcium chloride is that sufficient care was not taken to see that the calcium chloride was sufficiently dry in the earlier experiments.

The most interesting feature disclosed by the figures is the marked hysteresis shown on the return cycle over the hydrated calcium chloride (35 per cent. relative humidity) which, however, practically vanishes when the atmosphere of 75 per cent. relative humidity is again attained. This agrees with the latest work on the regain of cotton in which it is shown that absorption and desorption are reversible over short portions of the regain curves in the neighbourhood of saturation and of zero moisture content—Urquhart and Williams (3).

The last property which was investigated was density of wood substance and here also no decided difference was discoverable between the two classes of material, although the swamp kauri had on the average a somewhat lower density.

Densities were determined as follows. About 5 gm. of the sample was cut up into small cubes of sides of about 1 to 2 mm. The material was then waterlogged by soaking under distilled water under reduced pressure for a week to ten days to remove the contained air. The material was then weighed in a specific gravity bottle of 50 cm.^{3} capacity in boiled distilled water. After determining the oven dry weight the density of the wood substance of the sample of kauri was calculated at 15° C. after making any requisite temperature corrections.

Table IV.

Results of the determinations of the density of wood substance at 15° *C. of ten samples of kauri and four of swamp kauri. For comparison are given the determinations for three samples of common birch.*

Kauri pine	Swamp kauri	Common birch
1·485	1·494	1·512
1·513	1·504	1·502
1·512	1·497	1·520
1·525	1·516	—
1·534	—	—
1·486	—	—
1·532	—	—
1·530	—	—
1·495	—	—
1·503	—	—
1·512	1·503	1·511

The results of the determinations for ten samples of normal kauri and for four of swamp kauri are given in Table IV, which shows that on the average the density of the wood substance of swamp kauri is less than 1 per cent. lighter than that of the normal kauri. For comparison figures are given for three samples of the common birch (*Betula alba*).

The figure obtained for the density of wood substance by this method is not necessarily that of the wood substance itself but is the mean density of all the solid material of which the wood as a whole is composed. It must also be remembered that the density measured is that of wood substance in water which is about 5 per cent. higher than that of the dry material.

Similarly to starch, gelatine and other colloids when wood substance absorbs moisture the final volume of the damp material is somewhat less than the sum of the separate volumes of the material and of the moisture absorbed owing to the volume contraction that occurs on wetting—Volbehr (4).

In some recent work on swamp kauri Welch (5) has shown that kauri milled from these buried logs is liable to become worthless, due to damage which develops during seasoning and which reduced the tensile strength to the same value as the compression strength. This reduction in strength he attributes to the spiral checks or cracks which appear on the tracheid walls during the process of seasoning (presumably artificial seasoning). Some of Janka's experiments (1) are of interest in this connection since he showed that a period of two to three years' soaking in fresh or in salt water definitely reduced the compression strength of timber by somewhat over 5 per cent. when tested subsequently in the air dry condition; approximately 13 per cent. moisture content. He made, however, no microscopical comparison between the soaked timber and the controls.

Welch found no difference in the ash content, or in the rate of moisture loss or of moisture absorption between kauri pine and the swamp kauri.

Summary.

Swamp kauri was compared with normal kauri pine wood but no very decided differences between them were discoverable.

No definite structural differences were noted in the microscopic examination.

The shrinkage in swamp kauri was found to be less than in normal kauri when losing moisture under the same conditions.

No differences in hygroscopicity were noted.

The density of the wood substance of swamp kauri is the same or slightly less than that of normal kauri pine.

No mechanical tests were made.

The above investigation was carried out by the Forest Products Research Laboratory. I am indebted to the Director, Mr R. S. Pearson, C.I.E., F.L.S., for granting permission for publication.

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(*Received 13th April*, 1927.)

YIELD STUDIES IN OATS

II. THE RELATIONSHIP BETWEEN THE CHARACTERISTICS OF A SEED SAMPLE—ITS GERMINATION AND FIELD ESTABLISHMENT—AND THE EARLY GROWTH OF THE SUBSEQUENT PLANTS

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I. INTRODUCTION.

In a previous paper (7) reporting upon yield studies in oats, the influence of the parent crop upon the seed produced, its germination and subsequent growth, was shown to be one of the factors influencing the growth and yield of this cereal. It was found, for example, that the altitude at which the parent crop was grown influenced the panicle organisation and the quality and quantity of the grain produced; time of sowing of the parent crop was also shown to have an effect upon the seed qualities. The present paper forms a continuation of that study; the influence of the seed characters of commercial samples are considered.

Under normal economic conditions it is rarely an easy matter for the practical grower who purchases seed to obtain reliable information of potential value, as to the growth and environment of the parent crop; it is not always even possible to trace the parent crop. The farmer is therefore faced with the problem of selecting seed without such knowledge and is often forced to rely upon his own judgment of the seed as gauged by its apparent qualities re-enforced by germination data which are obtained through the provisions laid down in the Seed Act.

A study of a number of seed samples—of one variety, Record, believed to be a genetically pure type—has been undertaken in order to evaluate the importance from the standpoint of producing a good yield of those seed characters, which can be more easily ascertained.

For this purpose a number of samples from different environments were collected—and Wales possessing widely differing crop environments is a very suitable area from which to select. These samples were analysed and then grown together under normal conditions, so that growth data could be obtained.

II. THE COLLECTION OF THE SEED SAMPLES FROM DIFFERENT ENVIRONMENTS.

Twenty-five samples of grain were obtained from crops of Record oats grown in every Welsh county in the year 1926; some were from fertile lowland, others had been grown at surprisingly high elevations for *Avena sativa*. Although an attempt was made to obtain a natural sample as harvested, the absence of small grain (produced by the second flowers of the spikelets) in several cases indicated that some process of mass selection had been carried out in those samples particularly rich in large ("first") grain. For such reasons it was not possible to obtain all the data desired bearing on the question of the effect of "source of origin" upon the grain sample. Despite this, some interesting figures were observed in particular cases. From a crop grown at an elevation of 1200 feet above sea-level in the Llanarnion Duffryn Ceiriog district of Denbighshire the grain sample consisted almost entirely of extremely heavy first grain (no doubt some small second grain had been separated). The average weight per 100 dry caryopses of this sample was 31·69 gm. contrasting with a general figure of from 20–24 gm. It would appear that the number of grains per spikelet was reduced at this elevation. No data as to the number of spikelets per plant were obtained, but from previous work(6) it would seem probable that this number would be also reduced.

The moisture content of the samples varied from 12·5 to 17·2 per cent. The percentage husk varied from 23 to 28·5 per cent. Twenty-four of the samples were true to type—one was discarded on morphological grounds. A sample from a crop harvested in wet weather and stored so that the grain became heated was deliberately included in the series. This sample (Cc. 3069) gave very low germination figures and was outstanding on that account, so different was it from the remaining 23 samples (*i.e.* the deviation from the mean being exceptionally large) that frequently this sample determined the nature of the correlation coefficient between two sets of data. Calculations, omitting this sample (Cc. 3069), also have been made and wherever data for 23 samples are presented this is the one low germinating sample that has been omitted. By its very low germination and establishment figures a helpful extreme case has been provided for study.

III. THE METHODS ADOPTED FOR THE ANALYSIS OF THE SEED SAMPLE; COLLECTION OF SEED DATA.

(*a*) *Weight per* 1000 *grains*. The representative samples were carefully drawn by the approved method of the seed-testing stations and the average figure employed.

(*b*) *Moisture content, percentage husk and dry weight of caryopsis.* After husk removal of a sample of approximately 5 gm. weight, the caryopses were rapidly ground up and dried in an oven at 95° C. until constant weights were obtained. Drying *in vacuo* could not be carried out with so many samples (approximately 200). It was found that higher temperatures caused very slight increase in weight in the case of the ground caryopses if the drying was too prolonged, due no doubt to some oxidation. All moisture estimations both of the husk and caryopses were carried out in triplicate series. The percentage of husk to total is calculated upon the dry weight basis although it was only rarely found that the husk and caryopses differed in moisture content.

(*c*) *Sand germination tests—heating the grain.* These tests were carried out by the standard seed-testing method, using glazed earthenware saucers covered by slate. Five replications, *i.e.* five separate hundreds, of each sample were tested together. Another series of 500 seeds, which had been previously heated for 15 minutes at a temperature of 75° C. with all the grain spread out so as to acquire rapidly the oven temperature, was also tested.

IV. THE COLLECTION OF THE GROWTH DATA.

Five replicated rows of each sample of grain, both heated and control, were grown together in a vermin-proof cage. A particularly homogeneous plot of ground was selected for the experiment. The rows were arranged so that no given sample would be favoured by the position its rows occupied. The heated samples were separated from the controls as it was expected that several of these heated samples would give a low establishment percentage; had these rows been amongst the controls differential shading would have been unavoidable. It is believed that any (it must have been very small) differential shading between the control rows or the treated rows *per se* was compensated for by the chequer arrangement of the replications. The rows were spaced at a distance of one foot apart, 200 seeds were sown per row. Sowing took place on the 24th March.

Counts of the expanding first leaves were made at given intervals, the number of established plants was also estimated at frequent intervals. It was thought that data of value might be obtained by repeated inspection of the rows and the allocation of marks to each row upon a standard basis; such impressions as "general growth vigour" characterised by the amount of green leaf visible were regarded as a suitable basis for visual estimations. These inspection data were later carefully compared with absolute measurements including the number of plants, height and weight, and whereas they certainly conveyed a fairly good idea of the growth made they would not bear a detailed critical examination and therefore are not presented here.

As the experiment was designed primarily to trace out the effect of the seed characters upon early growth it was theoretically desirable, in the ideal case, to eliminate any other disturbing factors. In an attempt to meet this requirement it was decided to remove the plants for dry weight analysis before any competitive effects were apparent. Tillering, which does not take place to the same extent in every plant, begins very early at about the fourth week; it was thought that the effect of the seed characters would then still be apparent as indeed it has been demonstrated by other workers, Brenchley(1) and Findlay(3), that size of seed influenced *final* yield in annual crops. The plants were removed on June 1st before any tillers had withered; all the plants were in the same "growth stage"; they were "leafy" and no tillers had shown any signs of panicle formation. Inequalities in actual size of the plants of different samples will be considered in the discussion of the data.

Table I.

Showing the range of the figures used for the correlation coefficient calculations.

(1) *Seed data.*

	Weight per 1000 seeds gm.	% moisture content	Dry weight per 1000 caryopses gm.	% husk
Maximum	49·42	17·11	31·69	28·30
Minimum	30·42	12·52	19·05	23·47
Average	36·74	14·35	23·32	26·30

(2) *Sand test germination and field establishment data.*

Series	% germ. 4th day sand test	% total germ. sand test	% establish. seedlings, 3 weeks	% establish. plants, 10 weeks	Note
Control					
Maximum	87	98	38	37	* The poorest sample (Cc. 3069) included to provide an extreme case (see text).
Minimum	15*	24*	8*	10*	
Average	66	89	31	29	
"*Heated grain*"					
Maximum	81	97	38	34·5	
Minimum	2*	27*	8*	9*	
Average	43	88·5	29	26	

(3) *Growth data.*

Series	Dry weight of bulk obtained gm.	Average dry weight per 100 plants gm.
Control		
Maximum	262	82
Minimum	68	49
Average	179·5	65
"*Heated grain*"		
Maximum	285	84
Minimum	54	34
Average	152	57

Examination of the growing plants had proved that all, except one, of the 25 samples sown possessed the morphological characteristics of the type, *i.e.* Record, thus making the comparisons strictly legitimate.

It should be here pointed out that the dry weight of the top growth is here referred to as the "crop bulk" obtained. The roots were removed before drying, after the plants had been carefully counted. This bulk was obtained from 1000 seeds of each sample sown in rows and lifted ten weeks after sowing.

V. The analysis of the data by correlation studies.

In order to ascertain the relationship between the seed characteristics and early growth, coefficients showing the degree or correlation between the fluctuating seed characters on the one hand, and the growth data on the other were calculated. Dot charts of the data were prepared and carefully examined; it is possible to obtain apparently significant mathematical coefficients for series of data owing to the position of one or two readings when the remainder of the pairs give dots on the charts grouped almost at random in a very small given area of the chart. The influence of these samples and the absence of any *general* correlation is revealed by the charts. Fisher (4) has shown "how deceptive in small samples is the use of the standard error of the correlation coefficient, on the assumption that it will be normally distributed." "Without this assumption the standard error [method] is without utility." For this reason the standard error, or probable error, method of obtaining the probability of the coefficient has not been employed. The probability of each correlation coefficient has been easily obtained by means of the specially prepared tables for a small number of "pairs" given by Fisher (4) and is shown in brackets after each coefficient. When the probability (P) is low the correlation is regarded as significant. Many of the coefficients calculated have of course been rejected. Table II shows the significant correlation coefficients and those of no mathematical significance mentioned in the text. A duplicate series of calculations in which the very poorest sample (Cc. 3069) has been omitted has been carried out; in this series there are 23 pairs. It is emphasised that these 23 samples are normal commercial samples of oats procured from the practical growers.

V A. The Direct Correlation Coefficients.

(1) *The relation between seed characteristics and germination.* When the dry weight per 1000 caryopses figures were plotted against those of the percentage husk it was found that there was no significant arrangement: the values of the coefficients are:

For 24 samples, $R_{CL} = -\cdot 277 \qquad (P > \cdot 1)$.
For 23 samples, R_{CL}[1] $= -\cdot 162 \qquad (P > \cdot 1)$.

That is to say, the average size of "kernel" was not related to the percentage husk in these samples. The value of the coefficients of correlation

[1] The index letters refer to the data of Table II, *e.g.* C represents the dry weight per 1000 caryopses, L represents the percentage of husk; see pp. 406 and 407.

Table II.

The direct correlation coefficients obtained between seed characters and early growth data for 24 samples of Record oats showing the probability (P) of each coefficient. Calculations (omitting one special sample) are also shown for 23 samples.

	Reference	Dry weight per 1000 caryopses	% germination 4th day sand	% total germination sand	% seedlings established 3 weeks	% plants established 10 weeks	Total "bulk of crop" gm.	Average dry weight per 100 plants	% husk on seed
		C	*D*	*E*	*F*	*G*	*H*	*K*	*L*
Weight per 1000 seeds	*A*	—	(24) ·190 $P>·1$	(24) $P>·1$	—	(24) $P>·1$	(24) ·372 $P<·1>·05$	(24) ·513 $P<·02$	—
		—	(23) ·052 $P>·1$	(23) $P>·1$	—	(23) $P>·1$	(23) ·372 $P<·1>·05$	(23) ·535 $P=·01$	-
Moisture content of seed	*B*	(24) ·039 $P>·1$	(24) $-·458$ $P=·02$	(24) $-·413$ $P=·05$	(24) $P>·1$	(24) $>P·1$	(24) $P>·1$	—	—
		(23) ·107 $P>·1$	(23) $-·427$ $P=·05$	(23) $-·473$ $P=·02$	(23) $P>·1$	(23) $P>·1$	(23) $P>·1$	—	—
Dry weight per 1000 caryopses	*C*	—	(24) $-·135$ $P>·1$	(24) $P>·1$	(24) $P>·1$	(24) $P>·1$	(24) ·288 $P>·1$	(24) ·538 $P<·01$	(24) $-·277$ $P>·1$
		—	(23) $-·096$ $P>·1$	(23) $P>·1$	(23) $P>·1$	(23) $P>·1$	(23) ·135 $P>·1$	(23) ·514 $P<·02$	(23) $-·162$ $P>·1$

% germination 4th day sand test	*D*	—	—	(24) ·787 $P<·01$	(24) ·480 $P<·02$	(24) ·405 $P=·05$	(24) $P<·1$	(24) $P=·1$	(24) $P=·1$
		—	—	(23) ·435 $P<·05$	(23) $P>·1$	(23) $P>·1$	(23) $P>·1$	(23) $P>·1$	(23) $P>·1$
% total germination sand test	*E*	—	—	·	(24) ·805 $P<·01$	(24) ·724 $P<·01$	(24) ·573 $P<·01$	(24) −·583 $P<·01$	(24) $P>·1$
		—	—	· ·	(23) ·519 $P<·02$	(23) ·357 $P<·1>·05$	(23) ·280 $P>·1$	(23) $P>·1$	(23) $P>·1$
% seedlings established 3 weeks	*F*	-	—	—	—	(24) ·966 $P<·01$	(24) ·680 $P<·01$	(24) −·522 $P=·01$	(24) ·187 $P>·1$
		—	—	—	—	(23) ·899 $P<·01$	(23) ·485 $P=·02$	(23) ·186 $P>·1$	(23) ·153 $P>·1$
% plants established 10 weeks	*G*	—	—	—	—	—	(24) ·713 $P<·01$	(24) −·450 $P=·02$	· ·
		—	—	—	—	—	(23) ·551 $P<·01$	(23) −·085 $P>·1$	· ·
Total "bulk of crop"	*H*	—	—	—	—	—	—	(24) −·089 $P>·1$	· ·
		—	·	—	· ·	—	—	(23) ·297 $P>·1$	· ·

between the percentage germination in sand after four days and the percentage husk was not significant nor was any significant grouping found in the charts made:

For 24 samples, $R_{DL} = \cdot 344$ $(P = \cdot 1)$.
For 23 samples, $R_{DL} = \cdot 067$ $(P > \cdot 1)$.

Similarly the early seedling establishment estimations showed no significant relationship with the percentage husk:

For 24 samples, $R_{FL} = \cdot 187$ $(P > \cdot 1)$.
For 23 samples, $R_{FL} = \cdot 153$ $(P > \cdot 1)$.

The conclusion is therefore reached that in such commercial samples, inside one pure type—Record—the percentage husk bears no relationship to the germination of the samples.

No significant relationship was found between the size (weight estimation) of grain and sand germination—the values were as follows:

For 24 samples, $R_{CD} = - \cdot 135$ $(P > \cdot 1)$.
For 23 samples, $R_{CD} = - \cdot 096$ $(P > \cdot 1)$.
For 24 samples, $R_{AD} = - \cdot 190$ $(P > \cdot 1)$.
For 23 samples, $R_{AD} = \cdot 052$ $(P > \cdot 1)$.

The soil germination figures also showed no significant relationship with estimations of the size of the grain.

The average size of the caryopsis was not found to be related to the moisture content of the seed sample as is shown by these equations:

For 24 samples, $R_{BC} = \cdot 039$ $(P > \cdot 1)$.
For 23 samples, $R_{BC} = \cdot 107$ $(P > \cdot 1)$.

The correlation between the moisture content of the seed sample and the germination counts on the fourth day was a negative one:

For 24 samples, $R_{BD} = - \cdot 458$ $(P = \cdot 02)$. (1)
For 23 samples, $R_{BD} = - \cdot 427$ $(P = \cdot 05)$. (1 *a*)

The dot charts of the data indicated a general grouping of the results in a significant manner. When the total germination figures were considered along with the moisture content the equations obtained were:

For 24 samples, $R_{BE} = - \cdot 413$ $(P = \cdot 05)$. (2)
For 23 samples, $R_{BE} = - \cdot 473$ $(P = \cdot 02)$. (2 *a*)

The dot charts plotted from these readings also tended to indicate significance in these results; when therefore all the four equations and the two charts are considered together it can be safely concluded from them that samples stored in a moist condition do not germinate as well as samples which (by reason of better harvesting conditions) contain less

water; and that for this effect to be observed the moisture content need not be very high.

(2) *The influence of the factors "weight of seed" and "number of plants" upon growth.* The dry weight per 1000 caryopses, which is a direct measure of the food available for the seedlings, has been found to be correlated with the dry weight of the plants produced:

For 24 samples, $R_{CK} = \cdot 538$ $(P < \cdot 01)$. (3)
For 23 samples, $R_{CK} = \cdot 514$ $(P < \cdot 02)$. (3 *a*)

When the total weight per 1000 seeds was considered the value of the coefficient was not quite so high in the case of all the readings but was slightly higher when 23 readings were used, thus:

For 24 samples, $R_{AK} = \cdot 513$ $(P < \cdot 02)$. (4)
For 23 samples, $R_{AK} = \cdot 535$ $(P = \cdot 01)$. (4 *a*)

These results are in close agreement with the work of Brenchley (1) and others who have studied the large and small seed question in other crops. Previous work with oats carried out by the present writers had given similar results. The influence of the seed weight upon the individual plants was thus clearly discernible at this growth stage; towards the end of tillering.

When the total "crop bulk" was considered the direct coefficient between weight of seed and total crop was found to be much lower and of very doubtful significance.

These values of the coefficients between weight of seed and total crop were as follows:

For 24 samples, $R_{AH} = \cdot 372$ $(P < \cdot 1 > \cdot 05)$. (5)
For 23 samples, $R_{AH} = \cdot 372$ $(P < \cdot 1 > \cdot 05)$. (5 *a*)

In the case of the *dry* weight of the seed data smaller values were obtained:

For 24 samples, $R_{CH} = \cdot 288$ $(P > \cdot 1)$. (6)
For 23 samples, $R_{CH} = \cdot 135$ $(P > \cdot 1)$. (6 *a*)

Such values are of no significance. The influence of the weight of seed upon the growth of the individual plant was not apparent when the total crop yield was considered. The factor "number of plants" contributing to the yield had also to be taken into consideration.

A high degree of correlation existed between the number of plants and the mass of the total crop:

For 24 samples, $R_{GH} = \cdot 713$ $(P < \cdot 01)$. (7)
For 23 samples, $R_{GH} = \cdot 551$ $(P < \cdot 01)$. (7 *a*)

When the sample giving very poor germination and establishment was omitted the value of the coefficient was decreased; amongst the remaining 23 readings the range in establishment figures was very narrow. Somewhat smaller values were obtained for the coefficients of correlation between the earlier seedling establishment estimates and total crop:

For 24 samples, $R_{FH} = \cdot 680$ $(P < \cdot 01)$. (8)

For 23 samples, $R_{FH} = \cdot 485$ $(P = \cdot 02)$. (8 *a*)

Again the influence of the one very poorly germinating sample was considerable. The very high value of "R" obtained between the number of plants estimated at the first leaf stage, and when the plants were removed, indicates that in the interval of eight weeks, when once the plants were established, little differential killing or dying off took place. There was also no irregular delayed germination. These coefficients were:

For 24 samples, $R_{FG} = \cdot 966$ $(P < \cdot 01)$. (9)

For 23 samples, $R_{FG} = \cdot 899$ $(P < \cdot 01)$. (9 *a*)

It is pointed out that in this experiment the plants were protected from vermin, and free from disease, and that under other conditions, and in a less favourable season, there can be little doubt that more "casualties" would have occurred in an irregular way. When the total sand germination figures were considered with those of the weight of the crop a significant value was only found for the 24 readings:

For 24 samples, $R_{EH} = \cdot 573$ $(P < \cdot 01)$. (10)

For 23 samples, $R_{EH} = \cdot 280$ $(P > \cdot 1)$. (10 *a*)

When only those samples whose germination total was greater than 85 per cent. were considered the value of the coefficient of correlation between the total germination figures and total crop bulk was practically zero—

For "germination selected" 18 samples, $R_{EH} = \cdot 002$ $(P > \cdot 1)$.

This indicates that the high value obtained in equation (8) was caused by the few poor germination samples, and that for practical purposes, under such good conditions of soil and climate, samples having a sand germination total of 85 per cent. were as good as those having a higher germinating capacity.

The correlations between the sand test germination figures, and the percentage of plants established as seedlings three weeks after sowing, are given by the following figures (some of which are not shown in Table II): *4th day* germination figure and establishment:

For 24 samples, $R_{DF} = \cdot 480$ $(P < \cdot 02)$.

For 23 samples, R_{DF} is of no significance.

The influence of the poorest (germination) sample is very pronounced in this case.

The 5*th day* germination figures and establishment correlations were:

For 24 samples, $R = \cdot 677$ $(P < \cdot 01)$.
For 23 samples, $R = \cdot 313$ $(P > \cdot 1)$.

The correlation between the *total* sand germination figures and the percentage of plants established in the field was higher:

For 24 samples, $R_{EF} = \cdot 805$ $(P < \cdot 01)$. (11)
For 23 samples, $R_{EF} = \cdot 519$ $(P < \cdot 02)$. (11 *a*)

The high correlation coefficient was again caused by the samples of poor germination. When the samples of poor total germination were eliminated and those with a total of over 85 per cent. only considered, there was again found to be no correlation with the establishment in this narrow range of germination. It is interesting to observe that the final germination figures are more closely correlated with establishment than are the earlier figures. In a previous paper (10) evidence collected tended to show that rapidity of germination influenced establishment; in the commercial samples here tested no support is obtained for that view. When "the mean germination time" (*i.e.* time taken for 50 per cent. of the viable seeds to germinate) was plotted against the seedling establishment figures it was seen that only in the extreme cases of very poor germination was the time required correlated (negatively) with the soil establishment. The mathematical coefficient obtained is of very doubtful significance $R = -\cdot 313$ $(P > \cdot 1)$. It is here pointed out that in these "mean germination time" estimations the range of the time data was very narrow—the maximum was 4·0 days, the most rapid sample requiring 3·4 days. Unless the technique of sand germination tests is made more elaborate —which would probably reduce the number of possible tests—and subjected to many refinements it is not possible to obtain more accurate determinations of the mean germination time, as the intervals at which germination counts can be made are necessarily wide.

The value of the coefficients between total sand germination and *final* establishment was somewhat smaller than those previously considered in equations (9) and (9 *a*), where *seedling* establishment was considered:

For 24 samples, $R_{EG} = \cdot 724$ $(P < \cdot 01)$. (12)
For 23 samples, $R_{EG} = \cdot 357$ $(P < \cdot 1 > \cdot 05)$. (12 *a*)

For 18 selected samples with a high germination (of over 85 per cent.)

$$R_{EG} = 0 \text{ approx. } (12\,b).$$

In equation (12 *b*) the correlation between the number of plants established and the sand germination totals of samples germinating above 85 per cent. is shown to be practically zero. That is, for final establishment as for seedling establishment, a germination total of 85 per cent. in a sand test was as satisfactory as a higher figure under these growth conditions. It is apparent that over the wider ranges of germination totals (up to 85 per cent.), the sand tests afford reliable indications of the soil germination potentiality of the seed samples. Moreover, it is seen that the weight of produce obtained was, over the widest range of samples related closely to the number of plants established, and contributing to that total. When, however, comparisons were confined to samples of a high germination total no such correlations were found inside the narrower germination range of 85 to 100 per cent.

The relationship between the total "crop bulk" obtained and the size of the plant remains to be considered. The values obtained for this coefficient were too small to be of any significance:

$$\text{For 24 samples, } R_{HK} = -\cdot089 \quad (P > \cdot1). \qquad (13)$$
$$\text{For 23 samples, } R_{HK} = \cdot297 \quad (P > \cdot1). \qquad (13\,a)$$

It is of interest, however, to note that the omission of the sample which germinated poorly has caused a considerable change from a minus to a plus value. It has been previously observed in equations (7) and (8 *a*) that the total crop bulk was closely related to the number of plants, so that the relationship between the number of plants and the weight of the plants must be examined, as possibly this would be an indication of the intensity of the competition between the plants. The equations are:

$$\text{For 24 samples, } R_{FK} = -\cdot522 \quad (P = \cdot01). \qquad (14)$$
$$\text{For 23 samples, } R_{FK} = -\cdot186 \quad (P > \cdot1). \qquad (14\,a)$$

It is seen that for 23 readings the number of plants bears no relationship to the size of the plants at this stage; it must be noted here that the range in the number of plants was small. When the very poorest germinating sample was included there was a tendency for the weight of the plants to vary inversely as their number. It may be permissible, therefore, to conclude that in the extreme cases where germination was very low the size of the resultant plants was affected by the number. This would help to explain the change in sign of the coefficient in equations (13) and (13 *a*).

Table III.

Showing the partial correlation coefficients after eliminating one factor. The probability (P) is also indicated.

Equation reference Nos.	Factors for correlation coefficients	Factor reference	Factor eliminated	Reference	Values of R, 24 samples: Direct coefficient	Values of R, 24 samples: Partial coefficient	Values of R, 23 samples: Direct coefficient	Values of R, 23 samples: Partial coefficient
(3) and (3 *a*)	Dry weight of caryopses	*C*	—	—	$R_{CK}=\cdot538$ ($P<\cdot01$)	—	$R_{CK}=\cdot514$ ($P<\cdot02$)	—
	Dry weight of plants	*K*	Establishment	*G*	—	$R_{CK.G}=\cdot537$ ($P<\cdot01$)	—	$R_{CK.G}=\cdot513$ ($P<\cdot02$)
(4) and (4 *a*)	Weight of seed	*A*	—	—	$R_{AK}=\cdot513$ ($P<\cdot02$)	—	$R_{AK}=\cdot535$ ($P=\cdot01$)	—
	Dry weight of plants	*K*	Establishment	*G*	—	$R_{AK.G}=\cdot568$ ($P<\cdot01$)	—	$R_{AK.G}=\cdot547$ ($P<\cdot01$)
(5) and (5 *a*)	Weight of seed	*A*	—	—	$R_{AH}=\cdot372$ ($P<\cdot1>\cdot05$)	—	$R_{AH}=\cdot372$ ($P<\cdot1>\cdot05$)	—
	Dry weight of crop	*H*	Establishment	*G*	—	$R_{AH.G}=\cdot542$ ($P<\cdot01$)	—	$R_{AH.G}=\cdot388$ ($P<\cdot1$)
(6) and (6 *a*)	Dry weight of caryopses	*C*	—	—	$R_{CH}=\cdot288$ ($P>\cdot1$)	—	$R_{CH}=\cdot135$ ($P>\cdot1$)	—
	Dry weight of crop	*H*	Establishment	*G*	—	$R_{CH.G}=\cdot533$ ($P<\cdot01$)	—	$R_{CH.G}=\cdot185$ ($P>\cdot1$)
	Dry weight of plants	*K*	—	—	$R_{KG}=\cdot450$ ($P=\cdot02$)	—	$R_{KG}=-\cdot085$ ($P>\cdot1$)	—
	Establishment	*G*	Weight of seed	*A*	—	$R_{KG.A}=-\cdot531$ ($P=\cdot01$)	—	$R_{KG.A}=-\cdot158$ ($P>\cdot1$)
	Dry weight of plants	*K*	—	—	$R_{KG}=\cdot450$ ($P=\cdot02$)	—	$R_{KG}=-\cdot085$ ($P>\cdot1$)	—
	Establishment	*G*	Dry weight of caryopses	*C*	—	$R_{KG.C}=-\cdot463$ ($P<\cdot05$)	—	$R_{KG.C}=\cdot078$ ($P>\cdot1$)
	Establishment	*G*	—	—	$R_{GH}=\cdot713$ ($P<\cdot01$)	—	$R_{GH}=\cdot551$ ($P<\cdot01$)	—
	Dry weight of crop	*H*	Weight of seed	*A*	—	$R_{GH.A}=\cdot772$ ($P<\cdot01$)	—	$R_{GH.A}=\cdot559$ ($P<\cdot01$)
	Establishment	*G*	—	—	$R_{GH}=\cdot713$ ($P<\cdot01$)	—	$R_{GH}=\cdot551$ ($P<\cdot01$)	—
	Dry weight of crop	*H*	Dry weight of caryopses	*C*	—	$R_{GH.C}=\cdot784$ ($P<\cdot01$)	—	$R_{GH.C}=\cdot561$ ($P<\cdot01$)

V B. Partial Correlation Coefficients.

The direct relationship between the factors "number of plants," "weight of seed," and the weight of the resulting plants has been observed. In Table III the partial coefficients are shown after one factor has been eliminated.

By eliminating the "number of plants" (*i.e.* establishment) factor the coefficient of correlation between weight of seed and the weight of the resulting plants was increased, as is shown by these equations:

Direct coefficient for 24 samples, $R_{AK} = \cdot 513$ $(P < \cdot 02)$. (4)
Direct coefficient for 23 samples, $R_{AK} = \cdot 535$ $(P = \cdot 01)$. (4 *a*)
Partial coefficient for 24 samples, $R_{AK.G} = \cdot 568$ $(P < \cdot 01)$. (4 *p*)
Partial coefficient for 23 samples, $R_{AK.G} = \cdot 547$ $(P < \cdot 01)$. (4 *ap*)

The values of the partial correlation coefficients between the *dry* weight of the caryopses and the resulting plants obtained after eliminating the establishment factor are as follows:

Direct coefficient for 24 samples, $R_{CK} = \cdot 538$ $(P < \cdot 01)$. (3)
Direct coefficient for 23 samples, $R_{CK} = \cdot 514$ $(P < \cdot 02)$. (3 *a*)
Partial coefficient for 24 samples, $R_{CK.G} = \cdot 537$ $(P < \cdot 01)$. (3 *p*)
Partial coefficient for 23 samples, $R_{CK.G} = \cdot 513$ $(P < \cdot 02)$. (3 *ap*)

The establishment factor was also eliminated from the correlation between the weights of the seed and the total "crop bulk" obtained, thus:

Direct coefficient for 24 samples, $R_{AH} = \cdot 372$ $(P < \cdot 1 > \cdot 05)$. (5)
Direct coefficient for 23 samples, $R_{AH} = \cdot 372$ $(P < \cdot 1 > \cdot 05)$. (5 *a*)
Partial coefficient for 24 samples, $R_{AH.G} = \cdot 542$ $(P > \cdot 01)$. (5 *p*)
Partial coefficient for 23 samples, $R_{AH.G} = \cdot 388$ $(P > \cdot 1)$. (5 *ap*)

When the value of the coefficient of correlation between the dry weight of the caryopses and the total "crop bulk" were considered the effect of eliminating the establishment factor was found to be an increase in the value of "*R*." The probability figure was too high for equation (15 *ap*) to be of significance:

Direct coefficient for 24 samples, $R_{CH} = \cdot 228$ $(P > \cdot 1)$. (15)
Direct coefficient for 23 samples, $R_{CH} = \cdot 135$ $(P > \cdot 1)$. (15 *a*)
Partial coefficient for 24 samples, $R_{CH.G} = \cdot 533$ $(P < \cdot 01)$. (15 *p*)
Partial coefficient for 23 samples, $R_{CH.G} = \cdot 185$ $(P > \cdot 1)$. (15 *ap*)

These values were obtained when the more accurate measurements of the food reserves in the seed, the *dry* weight of the caryopses, were employed. The elimination of the establishment figures from the

equation for 24 samples has in both cases (*dry* weight of caryopses and seed weight, in equations (5 *p*) and (15 *p*) respectively,) given a significant coefficient with the crop bulk. In the 23 normal samples it is concluded from equations (5 *ap*) and (15 *ap*) that the weight of the seed was not closely correlated with the weight of the crop produced.

The correlation between the weight of the plants and the number of plants (establishment) is of no significance for the 23 samples, but of apparent significance for the 24 samples due to influence of the one sample of exceptionally poor germination. When the weight of the seed (*A*) and the *dry* weight of the caryopses (*C*) were in turn eliminated the values of the partial correlation coefficient between the number of plants and the size of the plants were of no significance. The actual values obtained are as follows:

Direct correlation for 24 samples, $R_{KG} = -\cdot 450$ $(P = \cdot 02)$. (16)
Direct correlation for 23 samples, $R_{KG} = -\cdot 085$ $(P > \cdot 1)$. (16 *a*)
Partial correlation for 24 samples, $R_{KG.A} = -\cdot 531$ $(P = \cdot 01)$.
Partial correlation for 23 samples, $R_{KG.A} = -\cdot 158$ $(P > \cdot 1)$.

where the "weight of seed" factor has been eliminated.

Partial correlation for 24 samples, $R_{KG.C} = -\cdot 463$ $(P < \cdot 05)$.
Partial correlation for 23 samples, $R_{KG.C} = -\cdot 078$ $(P > \cdot 1)$.

where the "dry weight of caryopses" factor has been eliminated.

The random distribution of the points on the dot chart indicated that there was no relation between the number of plants and their weight at this particular growth stage, when a narrow range of normal establishment figures was considered (see (16 *a*)). When the sample of very poor germination was included the greatly increased space per plant has caused the plants to be larger and a negative value of *R* was obtained (see (16)).

The weight of the "crop" has been shown to be closely correlated with the number of plants (equation (7)); when the effect of the weight of seed (*A*) and the *dry* weight of the caryopses (*C*) were eliminated the values obtained were increased:

Direct coefficient for 24 samples, $R_{GH} = \cdot 713$ $(P < \cdot 01)$. (7)
Direct coefficient for 23 samples, $R_{GH} = \cdot 551$ $(P < \cdot 01)$. (7 *a*)
Partial coefficient for 24 samples, $R_{GH.A} = \cdot 772$ $(P < \cdot 01)$.
Partial coefficient for 23 samples, $R_{GH.A} = \cdot 559$ $(P < \cdot 01)$.

where the "weight of seed" is eliminated.

Partial coefficient for 24 samples, $R_{GH.C} = \cdot 784$ $(P < \cdot 01)$.
Partial coefficient for 23 samples, $R_{GH.C} = \cdot 561$ $(P < \cdot 01)$.

where the "dry weight of caryopses" is eliminated.

VI. THE EFFECT OF HEATING THE SEED.

The seed samples were heated in a large drying oven for 15 minutes at 75° C. The seed was spread out so that the grain quickly acquired the oven temperature. The effect of this treatment upon germination and field establishment and growth was observed. As the heated samples of grain were not sown in the rows spaced amongst the control samples the soil growth and yield data of the two series were not critically compared. These samples, therefore, constituted a second series and correlation studies were therefore only of value within the series. The *general* effect of this short exposure to high temperature is shown in the following table:

	Control series	Treated series
Average 4th day sand germination	66 %	43·08 %
Average of "mean germination period*"	3·62 days	4·04 days
Average total germination	89 %	88·5 %
Average final field establishment	28 %	26·5 %
Average weight per 100 plants	65·1 gm.	57·2 gm.
Average total yield "per space unit" from 1000 seeds sown	182 gm.	152 gm.

* "Mean germination period" = time required for the germination of 50 % of the viable seeds of a given sample.

The heating treatment has retarded the rate of germination and reduced the number of plants established and has also decreased the average weight per 100 plants. These results are similar to those obtained by Groves (5), who exposed grain to high temperatures for varying periods.

VII. CORRELATION STUDIES.

A positive value, but of doubtful significance for the correlation coefficient between the moisture content of the seed and the reduction in the 4th day germination figure produced by heating was obtained.

$$\text{For all the samples } R = \cdot 368 \qquad (P < \cdot 1 > \cdot 05).$$

Other workers have also shown that the moisture content of the seed is related to the injury that occurs when samples of grains are heated.

That some protection was afforded by the husk was shown by the correlation coefficient between the reduction in the 4th day germination figures and the per cent. husk, the value of which was

$$R = - \cdot 370 \qquad (P < \cdot 1 > \cdot 05).$$

It would appear that the heavier seeds were more liable to injury by this treatment, for the correlation between seed-weight and the reduction in the number of the seeds germinating was positive.

Coefficient of correlation between weight per 1000 seeds and decrease in the 4th day germination figure,

For 24 samples, $R = \cdot 427$ $(P < \cdot 05)$.

Coefficient of correlation between *dry* weight per 1000 caryopses and decrease in 4th day germination figure,

For 24 samples, $R = \cdot 415$ $(P < \cdot 05)$.

The samples that germinate quickly (a high 4th day germination figure) were more susceptible to the injurious effect of the heating than samples germinating more slowly. The coefficient of correlation between 4th day germination figures of control samples and the decrease in the 4th day germination produced by heating the grain was:

For 23 samples, $R = \cdot 411$ $(P = \cdot 05)$.

It has been observed that the magnitude of the injurious effect of heating the grain was correlated with the size of the grain and also with the rate of germination of the sample under normal conditions. The weight of grain influenced the growth and weights of the control series of plants as shown by the earlier data in this paper. It was therefore thought that a positive correlation would exist between the magnitude of the injurious effect of heating as shown by germination figures, and the weights per 100 plants of the unheated (control) series. When calculated it was found to be of no significance, however,

$R = \cdot 322$ $(P > \cdot 1)$.

The relationship between the germination figures and establishment is shown by the following coefficients for the heated grain series:

Fourth day sand germination and seedling establishment in soil

$R = \cdot 063$ $(P > \cdot 1)$.

Fifth day sand germination and seedling establishment in soil

$R = \cdot 327$ $(P > \cdot 1)$.

Total sand germination and seedling establishment in soil

$R = \cdot 535$ $(P < \cdot 01)$.

If, however, only those samples of a germination of more than 85 per cent. were considered there was no correlation between total germination and establishment. The correlation between the early seedling establishment figures and the final establishment of larger plants was again high,

$R = \cdot 889$ $(P < \cdot 01)$.

The total "crop bulk" was closely related to "the number of plants" factor; the value for the series of this coefficient is

$R = \cdot 731$ $(P < \cdot 01)$.

In the control series the dry weight of the plants was found to be correlated with the weight of the seed and the amount of available food in the caryopsis. In the heated series the coefficient was of no material significance,

$$R = \cdot 252 \qquad (P > \cdot 1).$$

It would therefore appear that the heating had directly affected the availability of the food supply (or that an unforeseen disturbing factor had influenced the dry weights of these plants). The magnitude of the difference between the dry weight of the control plants and the dry weight of the plants from heated grain, gave too small a positive correlation

$$R = \cdot 296 \qquad (P > \cdot 1)$$

with the moisture content of the grain to show any tendency that most grain suffers most from this treatment, from this growth point of view (for germination effect see p. 416).

This treatment, heating the grain, influenced the "yield" by operating upon the "number of plants" factor. This was shown by the high value of the correlation coefficient between the decrease in the number of plants caused by heating and the decrease in the total bulk of the crop produced. These differences from the control figures were closely correlated

$$R = \cdot 728 \qquad (P < \cdot 01).$$

As a result of the preliminary work reported in a previous paper it was hoped that heating the grain and observing the effect upon germination might serve as a practical method of testing a sample's capabilities. Briefly, this extended trial has shown that a high moisture content is correlated with poor germination, and that such samples are probably more easily injured by the heating treatment. A "lively" quickly germinating sample was, however, susceptible to this injury; the heavy samples of high germination capacity have been also found to be more liable to injury. So that whilst further information can be obtained from the heating treatment it does not alone serve as a method of distinguishing undesirable samples.

VIII. GENERAL DISCUSSION.

There can be little doubt that there are two factors, contemporary for at least part of the growth period, influencing the size of the individual plants; these are the weight of the seed and the establishment (or germination total) factor. The influence of the seed is such that heavy seeds tend to produce large plants, whilst the influence of establishment, more clearly seen in the extreme cases, is such that low

germination figures tend to produce heavy plants. There is no evidence to show that these two factors operate one upon the other, that is, that heavy seeds necessarily germinate well; for it has been demonstrated that the correlation coefficients between the weight of the seed and the germination figures are of no significance. An attempt has been made to evaluate the influence of these two factors upon the growth of the individual plants and upon the total "crop bulk" obtained when estimated at this particular growth stage[1]. It is, of course, not assumed that the relative intensity of these two factors is constant for the entire growth period, or that they operate for an equal period; it is to be regretted that no oat data are available from which estimations of the degree of correlation between the size of seed and establishment on the one hand and growth on the other hand could be ascertained for any other growth stage than maturity (*i.e.* harvest data). The data here presented only show one point in the whole growth cycle. From *à priori* considerations it might be supposed that the weight of the seed factor would influence early growth more particularly and that the spacing factor, "establishment," would tend to show its maximum effect at a later developmental stage.

The data presented in this paper show that the weight of the plant is closely correlated with the weight of the seed, but when the whole crop bulk is considered the "number of plants," dependent upon germination and establishment, is the more closely correlated factor. Only in extreme cases does the additional space provided by very poor germination cause the weight of the plants to be increased, with normal germination and space this compensating power, a function of tillering is not revealed. Working with barley Engledow and Wadham (2) state that as a general rule the first formed is the largest and heaviest tiller so that $T_0 > T_1 > T_2 \ldots$, this is, in the opinion of the writers, applicable also to oats; so that the importance of a large number of plants each contributing one large tiller is emphasised. This conclusion is in agreement with previous work carried out by the writers with oats, as a result of which they emphasised the importance of establishment as a factor influencing yield in spring-sown oats in Wales.

Recently Pettinger (9) conducted a series of experiments to study the relationship of seedling characters and final yield. He measured the coleoptiles of the germinating seeds, but considered that other factors besides the amount of food stored influenced coleoptile length; he, however, fully realised that the seed weight influenced early growth in oats

[1] Tiller production was almost if not entirely completed; no small tillers had begun to wither, no signs of panicle production were observed.

and for his experiments used representative samples including large and small grain. No correlation of biological significance was found between coleoptile length and yield in the "Early Champion" material he employed. Other workers who have searched for an index of yield have compared various genetical types, but generally it may be said that no satisfactory index of yield has been found. Newman (8) reviews the Svalöf work from this point of view.

The data here discussed were obtained from Record oats which is believed to be genetically "pure." Inside such a variety samples of seed have been tested and the vigour of their early growth estimated. It has been shown that heavy or plump seed produce larger seedlings and that the number of plants determines the bulk of crop produced at one particular growth stage. It is not suggested that a similar result would be obtained with an exceptionally heavy tillering variety as "grey winter" or a "late" spring variety, but in this variety—Record—compensation for germination irregularities is not complete by any means when tiller initiation is completed. The importance therefore of a high percentage establishment is again emphasised.

SUMMARY.

A series of correlation studies has been carried out between the seed characteristics and early growth data of a number of Record oats samples; many coefficients of correlation obtained gave values of no biological significance. The influence of "outlying" readings had to be carefully considered as the number of readings was limited. For this purpose dot charts were employed as well as mathematical coefficients.

The results can be summarised as follows:

1. Generally the total germination figures in a sand test were correlated with field establishment, but within the narrow germination range 85–100 per cent. no correlation with establishment was found.

2. The amount of available food in the seed as measured by the average dry weight of the caryopses influenced the size and weight of the seedlings produced.

3. The moisture content of the grain was negatively correlated with the rate of germination, indicating that samples stored with a high water content did not germinate well.

4. The percentage husk bore no relation to germination.

5. Ten weeks after sowing the mass of the plants obtained from a given sowing depended primarily upon the number of plants established. Although tillering was well advanced plants possessing additional space

did not compensate for low establishment figures at this stage by increased growth.

6. When the grain was heated for 15 minutes at 75° C. those samples containing a high moisture content suffered more than well dried samples. Indications were also obtained that the following type of sample was particularly susceptible to such injury—artificial heating—

(*a*) a rapidly germinating sample,
(*b*) a thin-husked sample,
(*c*) a sample with heavy grain.

ACKNOWLEDGEMENTS.

The authors gratefully express their thanks to the County Agricultural Organisers and practical farmers for their kind help in procuring the samples and for the data supplied with the samples. They are deeply indebted to Prof. R. G. Stapledon for his stimulating interest in this work and for placing the facilities of The Welsh Plant Breeding Station at their disposal, and to Dr R. A. Fisher of Rothamsted, whose mathematical methods have been employed in this paper, for so kindly reading the manuscript prior to publication.

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(*Received 13th May*, 1927.)

SULPHUR TREATMENT OF SOIL AND THE CONTROL OF WART DISEASE OF POTATOES IN POT EXPERIMENTS

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(With 1 Text-figure.)

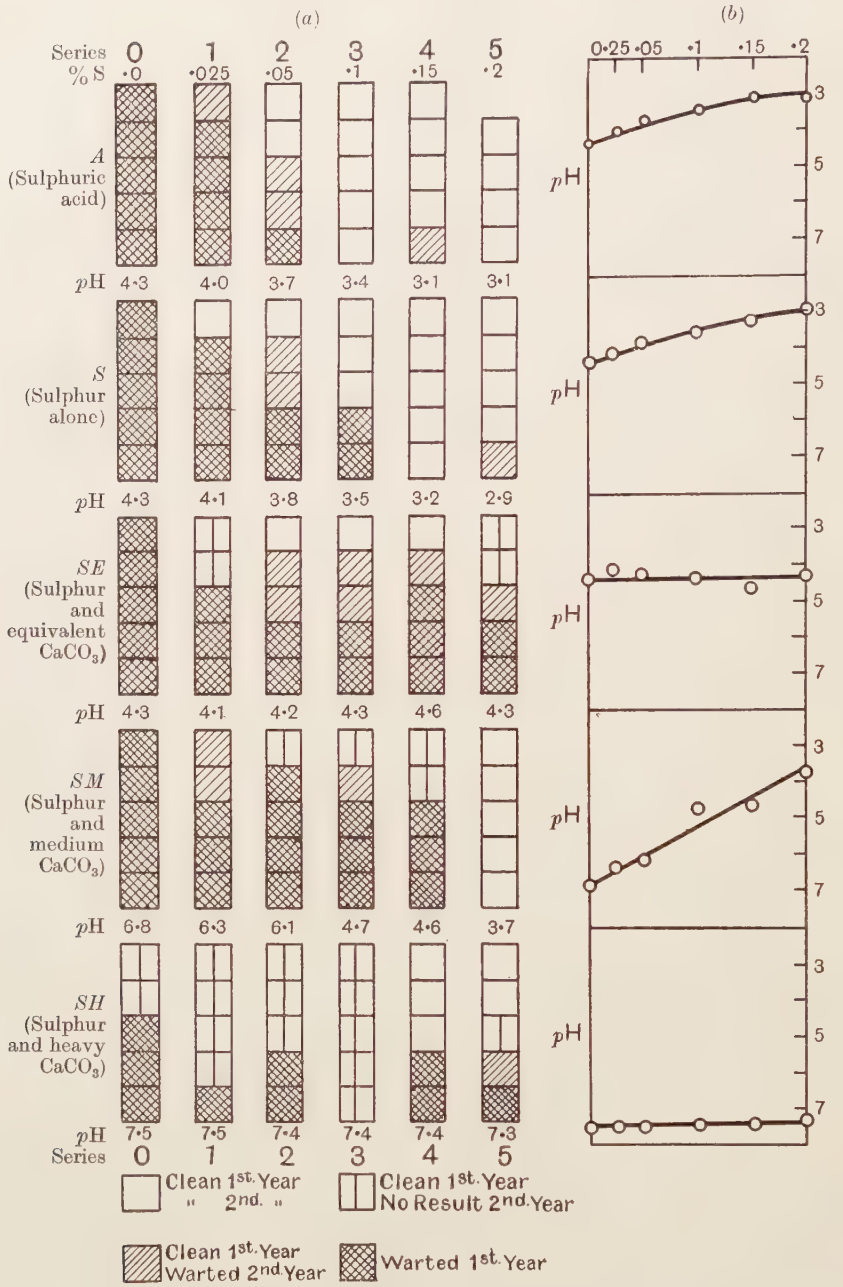
Field experiments described elsewhere(2) on potatoes grown in soil heavily contaminated with *Synchytrium endobioticum*, the fungus causing Wart Disease, have shown that thorough incorporation of finely divided sulphur with the soil may be followed by an almost clean crop of potatoes while neighbouring untreated plots give heavily infected plants. Since sulphur is oxidised to sulphuric acid in the soil, the treatment necessarily leads to an increased acidity except in those soils which contain large reserves of calcium carbonate. The question whether the toxicity of sulphur depends entirely on the development of a high degree of acidity or whether some other factor takes part has practical importance as well as theoretical interest. If a large increase in the soil acidity is necessary, the treatment will be impracticable owing to the high initial cost and the harmful effects on succeeding crops; if however the sulphur has some other mode of action, there remains the possibility of increasing its efficiency and of minimising the ill effects on later crops.

Evidence from field experiments has already been advanced to indicate that the toxic action is not a simple function of the final soil reaction(2). Mention was also made in this paper of a series of pot experiments which was planned to discriminate between two possible modes of action of sulphur, but which failed owing to the absence of infection in the crop grown. This experiment has now been carried out successfully and has afforded some further evidence in support of the hypothesis of a dual mechanism of sulphur toxicity.

Experimental.

The tests were carried out on potatoes grown in pots in an acid soil from Stalybridge, Cheshire, with which winter sporangia of the fungus were mixed. Each of five series of treatments consisted of 30 pots giving fivefold replicates of six different quantities of sulphur (0, ·025, ·05, ·1, ·15 and ·2 per cent. on the air-dry soil). In series *A* (Text-Fig. 1) the sulphur was added in the form of sulphuric acid in order to eliminate as far as possible the effects of intermediate compounds of sulphur. All the remaining series received finely ground sulphur, series *S* having sulphur only. In series *SE* the sulphur was accompanied by an equivalent amount of calcium carbonate to maintain an approximately constant final reaction so as to test the effects of possible intermediate compounds. A constant dressing of calcium carbonate was given to each pot in the *SM* series in an amount sufficient to bring the soil without sulphur almost to the neutral point. This dressing was equivalent to 0·15 per cent. sulphur so that treatments *SE* 4 and *SM* 4 were identical and were represented by a single set of 5 pots. Treatments *SM* 0 to *SM* 3 had an excess of calcium carbonate over sulphur, whilst treatment *SM* 5 had an excess of sulphur. Finally, in series *SH* a large excess of calcium carbonate (5 per cent.) was used so that a considerable amount remained and gave a slightly alkaline reaction even with the heaviest dressing of sulphur.

For each treatment 15 lbs. of soil, passing a 3 mm. sieve, were mixed thoroughly with 60 c.c. of a fine dry powder consisting of decayed warts and then with the appropriate chemicals; the additions and incorporation were carried out with the utmost care so as to ensure uniform distribution. Each 15 lb. lot of soil was divided equally between five ordinary flower pots and the whole series kept in a moist state. After four weeks one tuber of the highly susceptible variety, Arran Chief, was planted in each pot and the soil kept fairly moist for a further month, by which time shoots had appeared above the surface. From this time the soils were maintained in a very wet condition in order to favour infection(1). The soil proved to be difficult to wet, especially in the more acid series, and growth was so slow that it was considered advisable to allow five months after planting before lifting. By this time fairly good growth had taken place under each treatment. The pots which had given uninfected plants were kept in an air-dry state throughout the winter and in most cases a second crop of potatoes was grown in the following summer.


(a)
(b)
Series 0 1 2 3 4 5
% S ·0 ·025 ·05 ·1 ·15 ·2
A (Sulphuric acid)
pH 4·3 4·0 3·7 3·4 3·1 3·1
S (Sulphur alone)
pH 4·3 4·1 3·8 3·5 3·2 2·9
SE (Sulphur and equivalent $CaCO_3$)
pH 4·3 4·1 4·2 4·3 4·6 4·3
SM (Sulphur and medium $CaCO_3$)
pH 6·8 6·3 6·1 4·7 4·6 3·7
SH (Sulphur and heavy $CaCO_3$)
pH 7·5 7·5 7·4 7·4 7·4 7·3
Series 0 1 2 3 4 5
Clean 1st. Year
" 2nd. "
Clean 1st. Year
No Result 2nd. Year
Clean 1st. Year
Warted 2nd. Year
Warted 1st. Year
0·25 ·05 ·1 ·15 ·2
pH
3
5
7

Each square represents the result obtained in one pot.

Fig. 1. (*a*) Showing soil treatment, soil reaction and infection. (*b*) Showing percentage sulphur and soil reaction.

The numbers of clean and warted plants obtained after each treatment are set out diagrammatically in Fig. 1. Where for any reason as in most of the SH. series the growth in the second season was not sufficient to afford an adequate chance of infection, "no result" is recorded in the diagram. Electrometric determinations of the *p*H values of the soil were made after the first month and again after removing the first crops. These showed that the oxidation of the sulphur was almost complete in one month in all but the heaviest dressings. The *p*H values obtained when the crops were removed are entered under each column in Fig. 1*a*, and for ease of visual comparison are plotted in Fig. 1*b*, as a function of the amount of sulphur added.

Discussion.

The method adopted proved successful. Treatments A. 0, S. 0, SE. 0, in Fig. 1 represent 15 independent untreated pots every one of which gave an infected plant in the first year. With several of the treatments each of the five replicate pots gave uninfected plants in two seasons. The remaining treatments show a steady gradation between these extremes.

Sulphur (S.) and sulphuric acid (A.) have similar effects in reducing infection and in increasing the acidity. 0·1 per cent. sulphur as sulphuric acid and 0·15 per cent. sulphur as element and heavier dressings of either gave complete freedom from disease in the first year, and only 2 pots out of 24 became infected in the second year. This striking reduction of infection occurred when the acidity had exceeded that represented by *p*H 3·4, a degree of acidity somewhat higher than that put forward by Weiss(3) as the maximum acidity at which wart disease occurs viz. *p*H 3·9. This degree of acidity is considerably greater than that found in fertile arable soils, and there would be no opportunity of utilising sulphur as a practical soil treatment if its efficacy depended entirely on the development of an acidity exceeding some such limiting value.

An indication that sulphur reduces infection under conditions which preclude the production of such extreme acidities and which are thus more comparable with the field results is given by certain treatments in the present experiment. Thus in the SE. series the reaction in all cases is substantially the same as in the untreated soils, but half of the pots gave clean plants in the first year whilst all of the 14 untreated pots gave infected plants. Again in the series with a constant medium dressing of calcium carbonate, treatments SM. 1, SM. 2, and SM. 3 gave some

clean plants in the first year in soils which were less acid than the untreated soil. In the absence of sulphur this amount of calcium carbonate did not reduce infection. In SM. 5, with 0·2 per cent. of sulphur and calcium carbonate equivalent to 0·15 per cent. sulphur, there was no infection in either season although the final reaction approximated to that given by 0·05 per cent. sulphur, either as element or as sulphuric acid, and was less acid than that given by 0·1 per cent. sulphur as element. These smaller sulphur dressings however allowed appreciable infection.

In the presence of a large excess of calcium carbonate there was little infection in the first year, and even in the absence of sulphur two out of five pots gave clean plants. In an earlier experiment on potatoes grown in an artificially infected peat a few clean plants were obtained when very heavy dressings of calcium carbonate were applied. These results are in harmony with those of Weiss(3) in whose experiments infection was considerably reduced when the *p*H was 7·5 or more. Attention may also be drawn to the fact that wart disease appears to be more prevalent in the acid soils of semi-industrial areas than in the calcareous soils.

No explanation can be afforded at present for the absence of any connection between the extent of infection and the amount of sulphur in Series SE., SM. (excepting SM. 5) and SH.

Summary

In a series of pot experiments on potatoes grown in an acid soil artificially infected with the wart disease fungus, treatments with sulphuric acid and various combinations of sulphur and calcium carbonate, yielding a wide range of soil reaction, gave almost complete freedom from infection when the acidity of the soil had been raised to a very high value (*p*H 3·4 or less).

Heavy dressings of calcium carbonate, alone or with sulphur, giving a soil reaction of *p*H 7·5 or more, also reduced infection.

The fact that partial and even, in one experiment, complete suppression of disease was obtained at lower acidities, where the effect on the disease was not closely related to the degree of acidity, supports the tentative conclusion already drawn from field experiments that sulphur in controlling wart disease does not depend entirely on its effect in raising the acidity, but has also some other mode of action. Whether this toxicity which sulphur exerts apart from its effect on the acidity can be enhanced sufficiently to be of any practical value requires further investigation.

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(*Received June 2nd*, 1927.)

THE EFFECT OF HYDROGEN PEROXIDE ON YEAST GROWTH AND FERMENTATION

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(With 2 Text-figures.)

Yeast, with its accompanying enzymes, produces a vigorous fermentation under anaerobic conditions but multiplication of the yeast cells is greatly inhibited under these circumstances. Successful commercial propagation of yeast is attended by heavy aeration, by which means as high as 40 per cent. of the weight of nutrient used in the mash has been converted into yeast cells(1). A review of the literature dealing with the effects of aeration and other gases on yeast growth and fermentation has been given previously(2, 3). All of these former investigations were carried out under conditions which were essentially those most favourable for fermentation, rather than those which are best for rapid increase of yeast crop. The high yields of yeast under the favourable influence of heavy aeration may be due partly to the fact that yeast growth is aerobic in character. In this case, the optimum conditions would be those involving maximum interface between the gas and the mash. Aeration is also an efficient means of stirring whereby the yeast cells come into more intimate contact with their food. In studying the accelerative effect of aeration, it occurred to us that if the concentration of oxygen in the mash were the critical factor, it might be possible to produce the same acceleration by the gradual addition of hydrogen peroxide, at the same time substituting the mechanical effect of aeration by vigorous stirring. Hydrogen peroxide is rapidly decomposed by the catalase of the yeast with the formation of molecular oxygen and water, as is evidenced by the fact that if a suspension of yeast is added to 3 per cent. peroxide a rapid evolution of oxygen takes place. Our experiments show no favourable effect from the nascent oxygen thus introduced into the mash but demonstrate that the peroxide is exceedingly toxic, both to the yeast and to its accompanying enzymes. However, this toxicity

is only temporary, since yeast growth and fermentation proceed in a normal fashion after the peroxide has been removed by the action of the catalase.

Our experiments also compare the chemical changes and growth with and without aeration and confirm the accelerative effect of aeration reported by other investigators.

Experimental Part.

The general procedure in this series of experiments was the same as that described previously by one of us and A. K. Balls (2, 3). However, in the experiments described here only the principal chemical reactions taking place in the mash, such as changes in total solids, total sugar, rate of inversion (reducing sugar), yeast crop and *p*H were followed. These were determined exactly as before (2, 3). The yeast crop determination should be especially mentioned, however, since the actual dry weight of the yeast is recorded rather than the cell count which has been the usual index of yeast growth employed by others. It should also be noted that the total sugar is estimated as invert sugar and since it is present at the start chiefly as sucrose, the results reported for total sugar for the zero and second hours are too high by something less than 6 per cent.

At the beginning of each experiment, the various constituents of the mash were placed in a large specimen jar and thoroughly stirred by air introduced from a block tin pipe perforated with fine holes. A known quantity of yeast[1], in aqueous suspension, was then added and the contents of the flask diluted with water to the desired volume. To avoid errors due to evaporation, the air was first passed through two wash bottles to saturate it with water. All of the apparatus was kept in a thermostat at 28–28·5° C. After stirring for two minutes, the first samples were removed for analysis. The analysis was repeated after two hours; and after about four hours (the exact time is noted in each experiment) the mash was divided into three portions. The first part (A) served merely as a control and was untreated, aeration being continued as before. The second portion (B) consisted of a litre of mash, aerated in the same manner as the control, but treated with 30 per cent. hydrogen peroxide[2]. This addition was made very slowly at first, three cubic centimetres being added over a two hour period (fourth to sixth

[1] The yeast which was employed in these experiments was fresh baker's yeast, *Saccharomyces cerevisiae*, which was kindly furnished us by the Fleischmann Co.

[2] Superoxol, Merck.

Table I.

Experimental Data on Mashes.

Hour	Total sugar			Reducing sugar			Total solids			Yeast *a*			*p*H		
	A	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*C*
							Experiment I								
0	24·00	—	—	—	—	—	27·47	—	—	1·03	—	—	7·0	—	—
2	23·69	—	—	—	—	—	27·00	—	—	1·30	—	—	6·5	—	—
3·75	17·88	—	—	—	—	—	24·89	—	—	2·26	—	—	5·5	—	—
5·75	6·46	—	9·91	—	—	—	14·36	24·42	17·24	4·81	2·53	3·58	3·0‡	4·6‡	4·0‡
8	1·77	15·92	0·53	—	—	—	9·95	24·37	8·87	7·00	2·60	4·60	6·5	6·5	6·5
26	0·55	16·64	0·48	—	—	—	9·91	23·45	8·68	8·20	2·66	4·04	6·2	6·2	6·2
							Experiment II								
0	28·96	—	—	2·65	—	—	31·36	—	—	1·27	—	—	7·0	—	—
2	28·12	—	—	16·17	—	—	31·02	—	—	1·70	—	—	6·8	—	—
3·5	24·40	—	—	20·62	—	—	28·53	—	—	2·42	—	—	6·3	—	—
6·0	13·36	21·68	13·97	11·26	18·74	12·18	16·40	23·68	19·07	7·38	3·17	3·43	3·4‡	5·0	5·0
8·0	0·77	22·00	2·14	0·41	19·13	1·61	10·00	23·40	10·68	7·74*	3·32*	4·18*	—	—	—
26	0·38	0·40	0·93	—	0·40	—	9·52	8·88	8·18	9·27†	6·72†	—	6·0	4·8	4·8

* Analysis at 7·5 hour. † Analysis at 25 hour. ‡ Raised to *p*H 6·5 with $NaHCO_3$.

a Microscopical examination of the yeast was made at the time of each analysis to observe the general appearance of the yeast. No important infections were noted.

hour), while an additional 47 c.c. were added between the sixth and eighth hour. The third part (C) consisted of about 750 c.c. of the mash stirred without aeration, except for such air as unavoidably came into contact with the surface. Further analyses were made at the fourth, sixth, eighth and twenty-sixth hours. Fermentation in the control was practically complete at the end of the eighth hour.

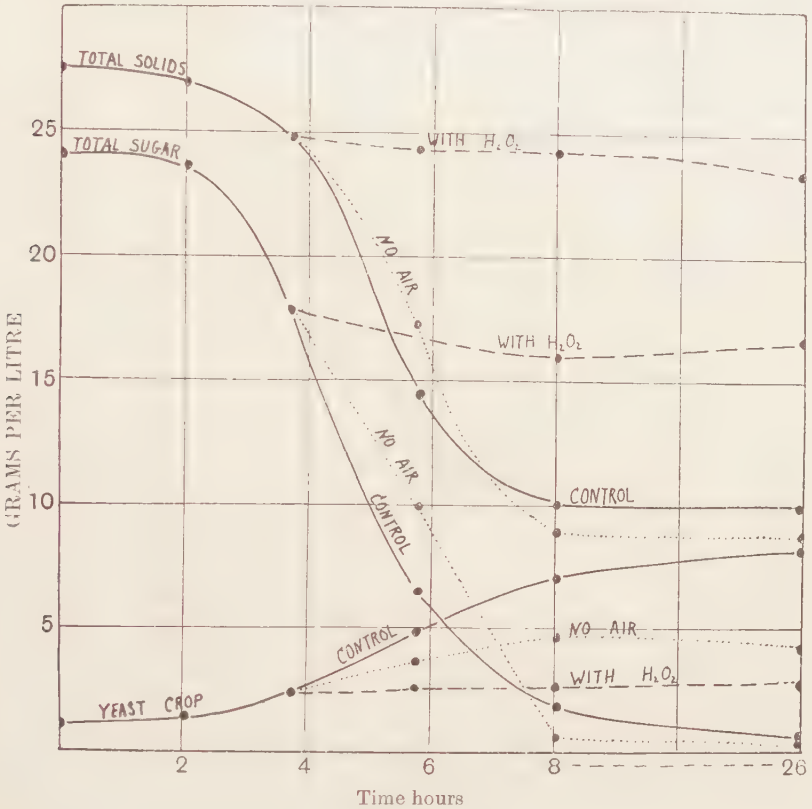

Fig. 1.

Only two typical experiments will be described here. Several trials similar to these two were carried out with like results, and it is unnecessary to show duplicate data.

Experiment I. Three litres of mash were made up as follows: molasses, 16; sucrose, 24; $(NH_4)_2HPO_4$, 1·2; $(NH_4)_2SO_4$, 1·6; yeast, 2·8 (all weights in grams per litre). At the beginning of the experiment the *p*H was adjusted to 7·0 by the addition of a few drops of sulphuric acid. Later on, when the *p*H had fallen, it was raised to 6·5 by the addition of small

amounts of sodium bicarbonate. The division into three mashes was made at the end of $3\frac{3}{4}$ hours. Lot one of the superoxol was used here. Results in Table I and Fig. 1.

Experiment II. This was an exact duplicate of (1) except that lot two of the superoxol was employed, and also that the second addition

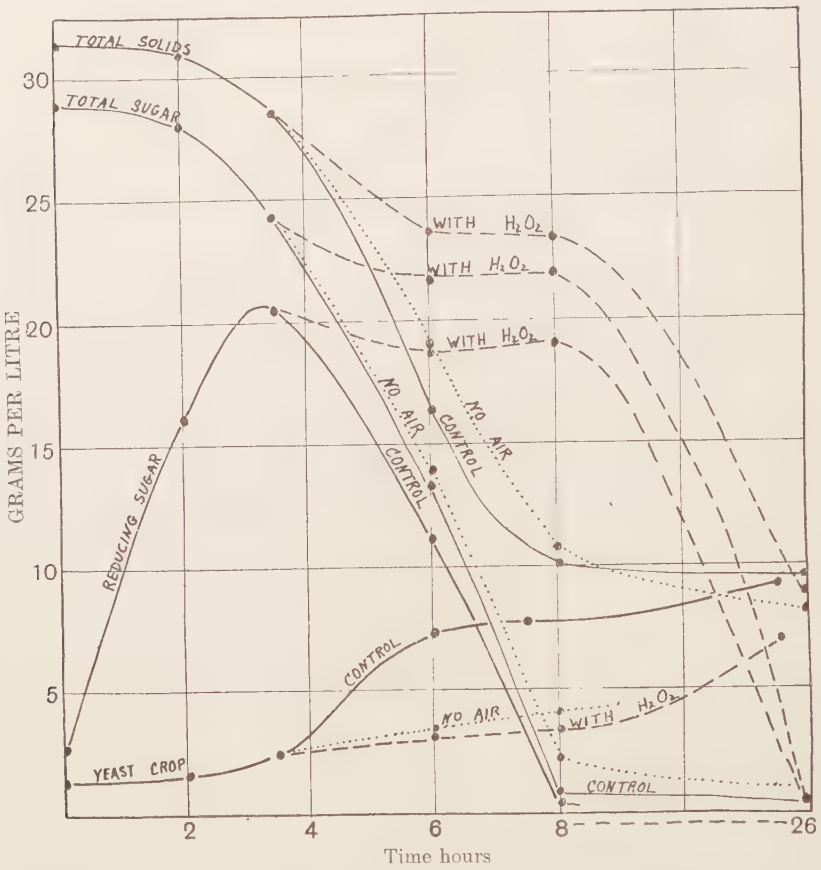

Fig. 2.

of superoxol was made in one portion of 47 c.c. at the sixth hour. It should be noted of course that new lots of yeast were used for each of the experiments. Since several trials of both Experiments I and II were made over a period of several weeks with different lots of yeast, it is reasonable to suppose that the variations are to be found in the peroxide rather than in the yeast. Results in Table I and Fig. 2.

Discussion of Results.

Our results, which can best be studied from the curves, demonstrate primarily the great toxicity of hydrogen peroxide for yeast[1]. Although only 3 c.c. of a 30 per cent. solution of peroxide were added during the first two hours, beginning at the fourth hour of the mash, yet there was marked inhibition of each of the important chemical changes occurring in the mash. The yeast growth was almost entirely stopped, the fermentation as measured by total solids and total sugars was greatly retarded, and even the inversion of sucrose by invertase stopped proportionately. During the second addition of 47 c.c. of peroxide over a period of two hours, there was practically entire cessation of all of these changes. However, the final total changes in Experiments I and II were quite different. In the case of Experiment I no recovery had appeared at the end of 26 hours, while in Experiment II almost complete recovery had taken place. We are at a loss to explain this difference. It is probable, however, that the explanation lies in the fact that the catalase of the yeast in Experiment I did not remove the peroxide as rapidly as in the second case. Such a condition would exist if the yeast were especially low in catalase, or if the peroxide contained an impurity inhibitory to catalase action. Chemical analysis of the peroxide showed for the first lot 0·23 gm. of solids per litre, and for the second 1·2 gms. per litre. This residue was largely made up of phosphates. Since several runs were made with each lot of peroxide, and since the yeast used in each run was from a different batch, it is not reasonable to assume a difference in the yeast or in the catalase content of the yeast. It is unfortunate that all of the first lot of the peroxide had been used before the difference was noted, since otherwise further chemical analysis of the ash might have answered this question.

Our experiments, showing the effect of lack of aeration on the rate of yeast growth and fermentation in a molasses mash, have been carried out in commercial laboratories, but so far as we know, have not been reported in the literature, except as noted in the introduction to this paper. The results, Mashes C, Table I, show a decided slowing of yeast multiplication and a much lower total final crop of yeast with practically no increase after the eighth hour. The rates of fermentation and inversion were affected only slightly, since they were complete in eight hours. It is worthy of note that with no aeration there was always a

[1] H. V. Euler and R. Nilsson (*Chem. Zelle u. Gewebe*, xii, 238 (1925) have very recently shown that hydrogen peroxide inhibits fermentation of glucose.

greater total loss of solids than under the other conditions we tried. We believe that this indicates that with no aeration the sugar is fermented more nearly to the theoretical fermentation equation than with aeration. Under aerobic conditions a small portion of the sugar is oxidised into non-volatile organic acids which partially accounts for the decided lowering of *p*H as the mash proceeds. In a number of the mashes, the data for which are not given here, we allowed the *p*H to change without added bicarbonate. In every case the *p*H fell from 7·0 to as low as 2·0 by the eighth hour, thus confirming the findings of H. Luers(4).

It was suggested to us that this very considerable souring of the mash might not be a normal process and that it might come about through contamination of the yeast with lactobacilli. We believe that a contamination sufficient to have produced enough lactic acid to cause such a lowering of *p*H would have been observed under the microscope. However, to prove the point, we performed a similar experiment, and used a pure culture of yeast, prepared for us by Prof. C. B. Morrey, of the Department of Bacteriology. The air was washed with bichloride of mercury and concentrated sulphuric acid before passing through the mash. The resultant *p*H was 2·5 in nine hours. The probable explanation of the high acidity lies in the fact that the yeast is utilising practically all of the ammonia from the ammonium sulphate and phosphate in the mash, resulting in the liberation of a small amount of free sulphuric and phosphoric acids. About 80 per cent. of the ammonia originally introduced is converted into yeast protein. We believe from these results that this great fall in *p*H is a normal process for the type of mash used.

The temporary toxicity of hydrogen peroxide for yeast and its enzymes is analogous, we believe, to the action of hydrocyanic acid. This acid also inhibits yeast growth and enzyme action as long as it is present, but as soon as the acid is removed by artificial means, growth and enzyme action are resumed. In the case of the peroxide, however, the removal of the toxic substance is brought about naturally by the catalase present.

Summary.

1. Hydrogen peroxide, when added in the form of superoxol to an aerated yeast molasses mash, is very toxic to the yeast, greatly inhibiting or entirely stopping yeast growth, fermentation and inversion.

2. The yeast yield without aeration in a mash of this kind is greatly diminished, while the other changes are only slightly inhibited, the total loss of solids being appreciably greater than with aeration.

3. If the *p*H change in such an aerated mash is allowed to progress normally, a marked fall from 7·0 to 2·0 is observed, apparently due to the formation of organic acids, and to removal of ammonia from the ammonium salts.

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(4) Luers, H. (1914). *Z. ges. Brauw.* xxxvii, 79.

(*Received* 31*st December*, 1926.)

THE EFFECT OF HEXYL RESORCINOL ON YEAST GROWTH AND FERMENTATION

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In connection with some studies on yeast metabolism we were interested in determining the toxicity of the new antiseptic, hexyl resorcinol, to ordinary baker's yeast, *Saccharomyces cerevisiae*. This new synthetic is noted both for its bactericidal action, having a phenol coefficient of 45–55, and for its proportionately low toxicity to animal organisms (2,3). For example, a rabbit can tolerate an oral dose of 1 gm. per kg. without harmful effect. There is no indication that it is more toxic to man. In practice it is possible by feeding an adult a gram of the substance in olive oil three times a day to produce actual bactericidal urine in the majority of cases. Our experiments demonstrate that hexyl resorcinol is as toxic to yeast as to bacteria, and further that concentrations of the antiseptic which entirely inhibit yeast growth also completely inhibit alcoholic fermentation.

Experimental Part.

Since we desired to follow both yeast growth and the chemical changes occurring in the mash, our experiments were arranged so as to facilitate making these determinations. The mash, four litres in volume, contained as follows:

Sucrose	96 gm.
Molasses	64 „
Diammonium phosphate	5 „
Ammonium sulphate	6·4 „
Yeast	11 „

The molasses was dissolved in 500 c.c. of water and centrifugalised to remove sediment. The sucrose was added to this solution and heated just to boiling. The ammonium salts were dissolved and boiled separately. At the beginning of the experiment these two practically sterile solutions were placed in a five litre specimen jar, the yeast in suspension in 50 c.c. of tenth normal sulphuric acid added, and the mixture diluted with

boiled tap water to exactly 4 litres. The fermentation was carried out under conditions favourable for rapid yeast multiplication, *i.e.* under heavy aeration, the air being introduced through a perforated block tin pipe in the bottom of the jar. The air had been previously passed through two wash bottles to saturate it with moisture at the temperature of the experiment, thus avoiding evaporation and change in composition of the mash from its source. The entire apparatus was kept in a thermostat at 28–28·5° C. When the mash had been thoroughly mixed by aeration for two minutes, two portions of 1 litre each were removed by siphon into two other aerating vessels. To these were added dropwise the required amounts of hexyl resorcinol[1] in 10 per cent. alcoholic solution. The rate of aeration was made as nearly equal as possible in the three vessels.

From time to time the three mashes were examined microscopically and analysed for total solids, total sugar, reducing sugar, and yeast crop. The methods used in these determinations are described in a previous paper(1). It is sufficient to state here that the first three components were determined in the centrifugalised beer, and that the yeast crops were estimated by filtering the mash through Gooch crucibles followed by two washings each with water and alcohol and drying for several hours at 107° C. The yeast crops therefore represent the weight of dry yeast substance. No cell counts were made.

In addition to the precautions for sterility described above, all of the containers were sterilised and the mashes kept covered during the experiment. The only sources of contamination would therefore come from the washed air or from the yeast itself. We employed ordinary bakers' yeast, supplied us by the Fleishmann Co. in pound lots. No contamination gross enough to appear under the microscope was found in any of our experiments. The results in our controls are practically identical with those we obtained in other experiments in which we used a pure culture of yeast and sterile air for aeration. On the other hand, the presence of slight infections which might result from the yeast used or from the air would in no way affect our conclusions arrived at in these experiments.

The analytical data and the results of these experiments are shown in Table I, the first series of data comparing the changes in a control and in mashes with 0·1 and 0·3 gm. of hexyl resorcinol per litre, and the second showing the effect of 0·01 and 0·005 gm. of the antiseptic per litre.

[1] Purchased from Sharp and Dohme, Baltimore, Md.

Table I.

(*All data in gms. per litre.*)

Hour of Analysis	*Experiment* 1			*Experiment* 2		
	Control	0·3 H.R.	0·1 H.R.	Control	0·01 H.R.	0·005 H.R.
			Total solids			
0	28·75	28·75	28·75	27·76	27·76	27·76
3	27·02	28·65	29·10	25·16	26·18	25·84
6	14·18	28·35	28·75	14·88	16·33	15·78
8	8·53	28·60	28·49	7·79	9·25	9·38
26	6·65	—	28·53	—	—	—
			Total sugar			
0	27·50	27·50	27·50	27·30	27·30	27·30
3	25·91	27·40	27·66	24·72	25·30	24·95
6	10·96	27·50	27·40	13·24	14·14	13·56
8	2·09	27·66	27·59	2·12	3·09	3·22
26	00·00	27·40	27·50	—	—	—
			Reducing sugar			
0	2·32	2·32	2·32	2·93	2·93	2·93
3	6·00	6·72	5·29	17·63	19·72	19·84
6	2·50	10·97	8·59	—	11·71	11·64
8	1·79	12·82	10·17	1·57	2·35	2·73
26	0·00	21·50	20·80	—	—	—
			Yeast crop			
0	0·91	0·91	0·91	0·86	0·86	0·86
3	1·86	0·74	0·90	1·91	1·67	1·75
6	4·56	0·58	0·96	4·61	3·90	4·15
8	5·62	0·77	0·90	6·37	5·28	5·80
26	7·19	0·62	0·84	—	—	—

Discussion of Results.

Concentrations of 0·3 and 0·1 gm. of hexyl resorcinol per litre completely inhibited yeast growth and fermentation as measured by loss of total solids and sugar. The higher concentration actually caused a slight loss in yeast weight while microscopically the cells appeared shrunken with no bud formation. It is noteworthy, however, that with each of these concentrations sugar inversion proceeded rapidly with little or no apparent inhibition of invertase action. Concentrations of 0·01 and 0·005 gm. of hexyl resorcinol per litre inhibit only slightly all of the changes, the degree of inhibition being roughly proportional to the amount of antiseptic present. Qualitative tests with fermentation tubes indicated that the sharp break in inhibition of fermentation occurred at a concentration of 0·025 gm. per litre.

From these results one may conclude that the antiseptic action of hexyl resorcinol to yeast is of the same order as that to bacteria, practically complete in 1–10,000. The fact that this antiseptic completely inhibits zymase action (intracellular enzyme) and is without effect on invertase (extracellular action) is of theoretical interest.

Summary.

1. Concentrations of 0·3 and 0·1 gm. of hexyl resorcinol per litre completely inhibit yeast growth and fermentation. Concentrations of 0·01 and 0·005 gm. only slightly inhibit.

2. Invertase action is not affected in the presence of 0·3 gm. of hexyl resorcinol per litre of mash.

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(*Received* 22*nd April*, 1927.)

EARLY MANIFESTATIONS OF POTATO BLIGHT (*PHYTOPHTHORA INFESTANS* DE BARY)

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(With Plate XXVI.)

The question of the origin of Potato Blight each year is of interest and the following observations seem of value as a corollary to the recent paper of Salmon(1).

On February 17th, 1927, a visit was paid to an experiment on rapid indoor infection of potatoes by Wart Disease for testing purposes at East Craigs carried out by Mr Anderson who said he was troubled by the wilting of potato shoots. The tubers were in a large, airy, well lighted laboratory at room temperature under conditions that, in the winter time especially seemed to indicate freedom from outdoor infection. The potatoes had been well washed, placed on sphagnum moss in saucers and watered at intervals: the whole experiment being carried on indoors. Among the tubers being tested for Wart Disease, several shoots were gathered, about eight in all, that appeared to be suffering from *Phytophthora infestans*, but were not producing spores. In all these shoots a large non-septate mycelium was found. One shoot was about 2 inches long, about $\frac{1}{3}$ inch thick and very sturdy and was infected from the base upwards for about $1\frac{1}{4}$ inches with a strong-growing non-septate mycelium. (A similar shoot is shown in Fig. 1.) One side of the shoot was flattened and browned in a typical *P. infestans* manner. From this area of the shoot, sections were taken and the mycelium was observed to start intercellularly. It formed the large lobular hyphae typical of *P. infestans* in the space where three host cells meet. In the more infected areas, the mycelium was intracellular. Small fragments of this tissue were placed in bog water (February 17th) and produced typical *Phytophthora* conidiophores (February 28th). Other shoots were affected towards the apex only, as if they were suffering from a secondary infection. Two or three diseased shoots were put in water in a damp chamber and in 24 hours the first had produced profuse *Phytophthora infestans* conidiophores (18th February). The others followed later with conidiophores.

Fig. 1. Tuber showing healthy shoots and a diseased shoot.

Fig. 2. Tuber showing diseased shoot.

ALCOCK & McINTOSH.—Early Manifestations of Potato Blight (pp. 440–441.)

On 25th February, a second visit was paid to Mr Anderson's laboratory. In three cases diseased shoots were producing the characteristic fructifications of *Phytophthora infestans*. Many infections were present also that were probably secondary. An especially common place of attack was the small buds in the leaf axils and also the leaves of the young shoots. A noticeable feature was the number of sprouts becoming infected on the under side of the potato, the side next to the sphagnum. These shoots did not progress far but soon rotted away.

It is unlikely in a laboratory during the winter that infection could come in from without. A possible source of infection is from conidiophores arising on the cut surface of tubers dealt with during the experiments in the laboratory. Although cases of slight infection with Blight have been seen, no conidia on the cut surface, nor extensive infection have been noticed; and all the tubers have been under close observation, both by Mr Anderson and by Miss Simpson.

The evidence points to initially infected shoots, proceeding from infected tubers, producing conidia and these conidia bringing about secondary infection on the other shoots that showed indication of being attacked at the apex first.

Observations would appear to support the theory of initial infection of potato shoots from the diseased tuber by the organism of late Blight *Phytophthora infestans* De Bary.

Summary.

Observations during February, 1927, are recorded on nominally healthy potato tubers sprouted indoors in the laboratory of the Seed Testing Station, East Craigs, producing short diseased shoots showing probable primary infection of *Phytophthora infestans*. At the end of the month probable cases of secondary infection occurred.

LITERATURE.

(1) Salmon, E. S. and Ware, W. M. (1926). *Ann. App. Biol.* xiii, No. 2, p. 289.

EXPLANATION OF PLATE XXVI.

Fig. 1. Sprouted potato tuber showing one shoot infected with *Phytophthora infestans*, infected from the base upwards. Probable primary infection from small original infection in tuber.

Fig. 2. Sprouted potato tuber showing infection of *Phytophthora infestans* in shoots; apex of shoot infected, probable secondary infection from infected shoots such as shown in Fig. 1. (At a late period shoots such as shown in Fig. 2 were fairly common.)

(*Received* 1*st May*, 1927.)

THE INSECT AND OTHER INVERTEBRATE FAUNA OF ARABLE LAND AT ROTHAMSTED. PART II

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(With 3 Text-figures.)

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1. Introduction.

The investigation which is described in the following paper was carried out between October 1923 and October 1924 and between April and November 1926. Its object was to ascertain the effects of dung and of various artificial manures with and without the addition of dung, on the soil fauna of arable land. A further object was to discover whether there was any noteworthy difference in the species present and their relative numbers and distribution in depth under these conditions as compared with their occurrence in the neighbouring field examined previously (6). The later part of this investigation, that carried out between April and November 1926, was done with a view to supplementing the information obtained earlier, and the results of the two periods are considered together. There had been no change in the manurial treatment of the plots in the interval, the only change being that in 1926 the mangolds were grown on the ridge, whereas previously they had been grown on the flat.

[1] Now Government Entomologist, Cyprus.

I am greatly indebted to Dr Imms for many helpful suggestions during the course of this investigation. I am also indebted to Miss K. Warington for information regarding the weeds; to Mr H. J. Page for the chemical analyses; to Dr B. A. Keen for the mechanical analyses; and for assistance in the identification of species of Insecta and "Myriapoda" to Messrs S. G. Brade-Birks, J. M. Brown, H. W. Ellis and G. T. Lyle.

2. Description of Area Examined.

The field in which the plots examined in the course of this investigation are situated is the Barn Field belonging to the Rothamsted Experimental Station, Harpenden. The soil, as in the case of the field previously examined here, is clay with flints overlying chalk. The Barn Field is roughly rectangular in shape with the long sides running S. by W. to N. by E., and, at its lowest part, the elevation is just above the 400 feet contour line.

The field is divided longitudinally into eight strips running the whole length of the field, each strip receiving one manure throughout its length. The strips are then subdivided into plots by cross-dressings of other manures, there being altogether 40 experimental plots.

Mangolds have been grown on this field since 1876 and in plots used in this investigation, the manurial treatment they receive and their yield of mangolds during 1924 are:

No. O 8, Unmanured (control): 2·14 tons.
No. A 8, Ammonium salts only: 10·18 tons.
No. O 5, Superphosphate only: 3·31 tons.
No. O 1, Dung only: 14·49 tons.
No. O 2, Dung, superphosphate and sulphate of potash: 18·61 tons.
No. A 1, Dung and ammonium salts: 20·75 tons.

The quantities of the different manures applied per acre are: dung 14 tons; ammonium salts 400 lb., consisting of equal parts of sulphate and muriate of ammonia of commerce; superphosphate 3·5 cwt.; and sulphate of potash 500 lb., this having been applied to Plot O 2 only since 1895. The "O" series of plots lies along the northern end of the field, and the "A" series lies across the field near the middle of its length. Each plot is rather over one-seventh of an acre in area. The effect of the different manurial treatments on the crop is very noticeable in their yield of roots and leaves, as well as in the general appearance of the mangolds and weeds.

The field was ploughed during the second week in February 1924.

Meteorological Conditions.

No records of meteorological conditions are given in the present paper. Barn Field adjoins the meteorological station of the Rothamsted Experimental Station and the records obtained here and elsewhere on the station are available. As these conditions would be more or less uniform for the different plots examined, they are not considered as part of the causes affecting the distribution of the fauna over the various plots.

3. Method of Investigation.

The samples of soil which were examined during this investigation were taken along one of the long edges of the plots, except on one or two occasions when the ground was snow-covered, samples being then taken well into the plots to avoid risk of missing the plot altogether. Successive samples from a plot were spaced well apart.

The samples were taken with the same apparatus of iron plates and trowel as was described previously(6); in addition a square iron frame was used which helps considerably to hold the plates in position whilst they are being driven into the ground. One side of this frame is removable, fitting into place over studs on the larger portion, this side being taken out to facilitate removal of the soil between the plates, this side of the frame and the smallest plate coming on the same side of the sample. The size of the frame is such that the plates will just fit inside it with a minimum of clearance, and slots are arranged in it to take the excess width of the largest plates, and hold them in position. With this frame in use it is considerably easier to drive the plates into the soil in their correct relative positions and the volume of soil enclosed by them is more likely to be correct, the plates being less liable to be displaced by striking against stones.

As before the samples of soil were each a nine inch cube, each sample being removed in five layers consisting of: I, the soil between the surface and a depth of one inch below the lowest point of the surface; II, the soil between a depth of one inch below the lowest point of the surface and a depth of three inches; III, the soil between three inches and five inches; IV, the soil between five inches and seven inches; V, the soil between seven inches and nine inches.

Each layer was placed in a linen bag and removed to the laboratory, where the soil was placed in the washing apparatus described previously (*Bull. Ent. Res.* xiii, 1922). If stirred constantly a bagful of soil could be completely washed in an hour or less, but usually it was more con-

venient to leave it longer, only stirring occasionally. After the washing was completed the residues on the two finer sieves of the apparatus were examined, a small portion at a time, in water in a white basin. The residue in the coarse sieve was also examined but did not require such detailed examination as that in the finer sieves, owing to the large size of any insects, etc., retained by it. Many forms floated on the surface of the water in the basin and the remainder could be readily seen through the clear water. Altogether 36 soil samples were taken. Seven samples of soil were examined from each of the plots without dung (O 8, A 8, O 5) and five samples from each of the plots with dung (O 1, O 2, A 1). The samples from the undunged plots were taken from October 1923 to March 1924, and those from the dunged plots from March to October 1924.

4. Soil Analyses.

The following table gives the mechanical analyses of the soil of the plots:

Plot numbers and depth of samples	Water in air dry soil %	Loss in solution %	Coarse sand %	Fine sand %	Silt %	Fine silt I %	Fine silt II %	Clay %	Loss on ignition %
O 8 surface to 5″	1·9	0·9	8·9	18·4	27·4	5·6	2·6	23·6	7·2
5″ to 9″	3·3	0·9	6·2	13·9	20·4	7·0	1·2	36·4	8·3
A 8 surface to 5″	1·9	0·7	6·7	21·9	34·8	10·0	4·6	20·8	5·9
5″ to 9″	3·3	0·7	4·2	16·2	24·6	6·8	2·8	33·6	7·4
O 5 surface to 5″	2·0	1·1	8·2	20·7	29·0	11·2	0·8	20·6	6·7
5″ to 9″	2·5	1·1	8·9	18·5	23·4	7·6	3·2	27·2	6·6
O 1 surface to 5″	2·6	1·0	7·1	15·8	27·8	7·6	2·0	23·6	9·8
5″ to 9″	3·2	0·6	5·7	14·4	23·4	7·2	2·6	32·8	9·1
O 2 surface to 5″	2·3	1·0	7·4	18·1	8·6	27·8	1·6	22·0	9·7
5″ to 9″	3·3	0·5	4·3	13·1	19·6	11·4	0·6	35·4	8·6
A 1 surface to 5″	2·5	1·0	8·2	19·4	29·0	9·6	2·2	18·6	9·1
5″ to 9″	2·0	0·9	7·2	19·3	30·2	9·2	3·0	17·4	7·9

Chemical analyses have also been obtained of the soil of the plots, but as they do not indicate any very important differences between the various plots which can be correlated with differences in the soil fauna, it is not considered necessary to publish them. These figures are however being kept so that they can be referred to at any time if necessary.

5. Occurrence of Weeds.

Weeds are usually fairly abundant on Barn Field, although only a few species are important. Owing to the nature of the crop, cleaning operations can be carried out quite conveniently during most of the year, so that there is never a mass of weeds such as is found on Broadbalk.

Cirsium arvense is the only important perennial; of the plots under consideration it is most plentiful on those not receiving dung. *Capsella bursa-pastoris* and *Veronica hederaefolia* are abundant, and *Stellaria media* is also important.

6. Soil Fauna of Experimental Plots Subjected to Varied Kinds of Manuring.

In the following lists the worms have been divided into two groups, those belonging to the sub-order Terricolae of the order Oligochaeta, which includes the true earthworms, *Lumbricus*, etc., forming one group as Oligochaeta (Terricolae), and all other worms, probably principally belonging to the family Enchytraeidae of the Oligochaeta, and to the Nematoda, forming the second group as Oligochaeta (Limicolae), etc.

The numbers following the names have the following meaning: the first numbers give the months during which the species was met with; the first numbers within the brackets give, above, the total number found, and below, in Roman numerals, the levels in which they were found. The second numbers within the brackets give, above, the greatest number found at any one level, and below, in Roman numerals, the level at which they were found.

Thus—*Onychiurus fimetarius* (L.) 3, 4, 5, 6, 10 $\left(\frac{26}{\text{I–V}}, \frac{11}{\text{II}}\right)$ indicates that this species was found in the months March to June and October; 26 were found altogether, occurring in each of the five layers, from the surface to a depth of nine inches; and 11 of these were found in the second layer, between a depth of one inch and three inches.

The species of Insects and other Invertebrates present in the plots were as follows:

Plot No. O 8. *Unmanured (Control).*

Samples taken in months 10, 11, 12, 1, 2, 4, 6, 10.

INSECTA.

Collembola. *Onychiurus armatus* (Tullb.) 11, 12, 1, 2, 4, 6, 10 $\left(\frac{36}{\text{I–III}}, \frac{19}{\text{II}}\right)$; *Achorutes purpurescens* Lubb. 11, 12 $\left(\frac{6}{\text{II, V}}, \frac{4}{\text{V}}\right)$; *Isotoma grisescens* Schäff. 10 $\left(\frac{1}{\text{I}}\right)$; *I. minor* Schäff. 10 $\left(\frac{4}{\text{V}}\right)$; *Orchesella villosa* (Geoff.) 6 $\left(\frac{1}{\text{IV}}\right)$; *Lepidocyrtus cyaneus* Tullb. 6 $\left(\frac{1}{\text{III}}\right)$.

Psocoptera. Sp. 10 $\left(\frac{1}{\text{II}}\right)$.

Thysanoptera. Sp. 4, 10 $\left(\frac{2}{\text{III}}\right)$.

Hemiptera. *Anthocoris nemoralis* F. 10 $\left(\frac{1}{II}\right)$.

Coleoptera. *Helophorus nubilus* F. 11 $\left(\frac{1}{II}\right)$; *Atheta* (*Meotica*) *exilis* Er. 1 $\left(\frac{1}{I}\right)$; *Homalota* sp. 4 $\left(\frac{1}{II}\right)$; *Aleochara* sp. 4 $\left(\frac{1}{I}\right)$; *Oxytelus tetracarinatus* Block. 6 $\left(\frac{2}{IV\text{–}V}\right)$; *Scopaeus sulcicollis* Steph. 12 $\left(\frac{1}{IV}\right)$; *Atomaria linearis* Steph. 12, 2, 10 $\left(\frac{4}{III\text{–}V}, \frac{2}{III}\right)$; *Anthicus antherinus* L. 2 $\left(\frac{1}{II}\right)$; *Ceuthorrhynchus quadridens* Panz. 4 $\left(\frac{1}{IV}\right)$. Larvae: Sp. 10 $\left(\frac{1}{III}\right)$; Carbidae 10, 1 $\left(\frac{3}{I\text{–}III}\right)$; Nebria sp. 1, 2 $\left(\frac{2}{I}\right)$; Staphylinidae 10 $\left(\frac{1}{I}\right)$; Elateridae, *Agriotes* sp. 10 $\left(\frac{1}{III}\right)$.

Diptera. Cecidomyidae. Larvae in grass stem sp. 1 $\left(\frac{2}{I}\right)$, larvae sp. 4 $\left(\frac{1}{IV}\right)$. Scatopsidae. Sp. (larvae) 6 $\left(\frac{1}{III}\right)$. Empidae. Sp. 6 $\left(\frac{1}{IV}\right)$. Phoridae. *Phora* sp. 6 $\left(\frac{1}{IV}\right)$; sp. 10 $\left(\frac{1}{II}\right)$. Borboridae. *Limosina* sp. 6 $\left(\frac{1}{II}\right)$. Anthomyidae. *Leptohylemyia coarctata* Fall. (eggs) 10, 12, 1 $\left(\frac{5}{I, II}, \frac{3}{I}\right)$.

Hymenoptera. Formicidae. Sp. 6 $\left(\frac{1}{I}\right)$. Braconidae. *Blacus* sp. 10 $\left(\frac{1}{II}\right)$.

DIPLOPODA. Non det. 10, 11, 12 $\left(\frac{9}{I\text{–}V}, \frac{3}{III}\right)$. Polydesmidae. Sp. 4, 10 $\left(\frac{5}{I\text{–}III}, \frac{2}{II, III}\right)$. Blaniulidae. (Probably mainly *Blaniulus guttulatus* (Bosc.), 10, 2, 4, 6 $\left(\frac{13}{I\text{–}V}, \frac{4}{III}\right)$.

SYMPHYLA. Sp. 10 $\left(\frac{1}{V}\right)$.

ARACHNIDA. Araneida. Sp. 11, 12, 6 $\left(\frac{3}{I}\right)$.
Acarina. Sp. 10, 11, 12, 6 $\left(\frac{4}{I\text{–}V}\right)$.

OLIGOCHAETA (Terricolae). 10, 4 $\left(\frac{3}{I, IV, V}\right)$.

OLIGOCHAETA (Limicolae). 4, 6, 10 $\left(\frac{29}{I\text{–}V}, \frac{12}{II}\right)$.

ISOPODA. 11 $\left(\frac{2}{III, IV}\right)$.

Plot No. A 8. (*Ammonium Salts.*)

Samples taken in months 11, 12, 1, 2, 3, 4, 5, 10.

INSECTA.

Collembola. *Anurida granaria* (Nic.) Tullb. 12, 1 $\left(\frac{2}{II, III}\right)$; *Onychiurus armatus* (Tullb.) 11, 12, 1, 2, 4, 10 $\left(\frac{75}{I\text{–}V}, \frac{45}{II}\right)$; *O. fimetarius* (L.) 2 $\left(\frac{1}{IV}\right)$; *O. ambulans* (L.) 12 $\left(\frac{2}{IV}\right)$; *Achorutes purpurescens* Lubb. 11, 1 $\left(\frac{2}{V}\right)$; *Isotomurus palustris* (Mulls.) 11 $\left(\frac{1}{I}\right)$; *Entomobrya nivalis* (L.) 1 $\left(\frac{1}{III}\right)$.

Orthoptera. *Ectobius lapponicus* L. 11 $\left(\frac{1}{V}\right)$; *Forficula auricularia* L. 11, 3 $\left(\frac{2}{II, III}\right)$, eggs 3 $\left(\frac{36}{III}\right)$.

Thysanoptera. Sp. 11, 10 $\left(\frac{3}{I}\right)$.

Hemiptera. Sp. (larva) 5 $\left(\frac{1}{III}\right)$. APHIDIDAE Sp. 10 $\left(\frac{2}{I}\right)$.

Coleoptera. *Xantholinus punctulatus* Payk. 5 $\left(\frac{1}{III}\right)$; *Oxytelus tetracarinatus* Block 4 $\left(\frac{1}{III}\right)$; *O. inustus* Grav. 5 $\left(\frac{1}{IV}\right)$; *O. nitidulus* Grav. 10 $\left(\frac{1}{III}\right)$; *Stenus subaenus* Er. 1 $\left(\frac{1}{I}\right)$; *Trichopteryx* sp. 4 $\left(\frac{1}{III}\right)$; *Euplectus piceus* Mots. 5 $\left(\frac{1}{IV}\right)$; *Atomaria linearis* Steph. 10 $\left(\frac{1}{IV}\right)$. Larvae: CARABIDAE 11 $\left(\frac{2}{I, II}\right)$; STAPHYLINIDAE 4, 10 $\left(\frac{2}{I, II}\right)$.

Diptera. CECIDOMYIDAE. Sp. (larva) 4 $\left(\frac{1}{IV}\right)$, (pupa) 4 $\left(\frac{1}{III}\right)$. MYCETOPHYLIDAE. Sp. 3 $\left(\frac{1}{III}\right)$. CHIRONOMIDAE. Sp. (larvae) 4, 5 $\left(\frac{3}{I, II}, \frac{2}{I}\right)$. TIPULIDAE. *Trichocera* sp. (larvae) 2, 4, 5 $\left(\frac{7}{II–IV}, \frac{3}{IV}\right)$. BIBIONIDAE. *Dilophus* (larvae) 2 $\left(\frac{6}{I–II}, \frac{5}{II}\right)$. ANTHOMYIDAE. Sp. (pupa) 10 $\left(\frac{1}{I}\right)$; *Leptohylemyia coarctata* Fall. (eggs) 11, 12, 1, 10 $\left(\frac{27}{I–III}, \frac{19}{I}\right)$.

Hymenoptera. BRACONIDAE. Sp. 5 $\left(\frac{1}{I}\right)$.

DIPLOPODA. Non det. 11, 12 $\left(\frac{2}{II, III}\right)$. *Ophiodesmus albonatus* (Latzel) 3 $\left(\frac{1}{V}\right)$. BLANIULIDAE. Sp. 4 $\left(\frac{1}{II}\right)$.

ARACHNIDA. Araneida. Sp. 4 $\left(\frac{1}{III}\right)$.

Acarina. 11, 12, 4 $\left(\frac{19}{II, III}, \frac{18}{III}\right)$.

OLIGOCHAETA (Terricolae). 5, 10 $\left(\frac{2}{I, II}\right)$.

OLIGOCHAETA (Limicolae). 11, 4, 5, 10 $\left(\frac{44}{I–V}, \frac{19}{II}\right)$

Plot No. O 5. *Superphosphate only.*

Samples taken in months 11, 12, 1, 2, 3, 4, 6, 11.

INSECTA.

Collembola. *Anurida granaria* (Nic.) Tullb. 11, 1 $\left(\frac{2}{III, IV}\right)$. *Onychiurus armatus* (Tullb.) 11, 12, 1, 2, 5, 6, 11 $\left(\frac{141}{I–V}, \frac{59}{II, III}\right)$; *O. ambulans* (L.) 11 $\left(\frac{5}{IV}\right)$; *Achorutes purpurescens* Lubb. 11, 12 $\left(\frac{9}{I, III, IV}, \frac{4}{III, IV}\right)$; *Entomobrya muscorum* (Tullb.) 1 $\left(\frac{1}{II}\right)$; *E. marginata* Tullb. 6 $\left(\frac{1}{III}\right)$; *Isotomurus palustris* (Mull.) 12 $\left(\frac{1}{I}\right)$.

Thysanoptera. Sp. 5 $\left(\frac{1}{I}\right)$.

Hemiptera. APHIDIDAE. Sp. 6 $\left(\frac{1}{I}\right)$.

Lepidoptera. NOCTUIDAE. Sp. (Larva) 11 $\left(\frac{1}{I}\right)$.

Coleoptera. *Helophorus Mulsanti* Rye 6 $\left(\frac{1}{\text{III}}\right)$; *Homalota* sp. 5, 6 $\left(\frac{3}{\text{I, IV, V}}\right)$; *Oxytelus nitidulus* Grav. 11 $\left(\frac{1}{\text{III}}\right)$; *Atomaria linearis* Steph. 11 $\left(\frac{2}{\text{IV, V}}\right)$; *Haltica* sp. 11 $\left(\frac{1}{\text{I}}\right)$. Larvae: Carabidae 11, 1 $\left(\frac{2}{\text{II, III}}\right)$; Staphylinidae 11 $\left(\frac{1}{\text{I}}\right)$; sp. 11 $\left(\frac{1}{\text{II}}\right)$.

Diptera. Cecidomyidae. (Larva) 1 $\left(\frac{1}{\text{I}}\right)$. Tipulidae. Sp. (larva) 11 $\left(\frac{1}{\text{I}}\right)$; *Trichocera* sp. (larva) 11 $\left(\frac{2}{\text{II}}\right)$. Scatopsidae. Sp. (larva) 11 $\left(\frac{1}{\text{III}}\right)$. Anthomyidae. *Leptohylemyia coarctata* Fall. (eggs) 1, 11 $\left(\frac{3}{\text{I, II}}, \frac{2}{\text{II}}\right)$. Muscidae. Sp. (parasitised puparium) 11 $\left(\frac{1}{\text{I}}\right)$.

Hymenoptera. Formicidae. *Donisthorpea flava* F. 11 $\left(\frac{1}{\text{II}}\right)$. Braconidae. *Alysia rufidens* Nees. 11 $\left(\frac{1}{\text{I}}\right)$ (reared from Muscid puparium).

CHILOPODA. *Geophilus longicornis* Leach 5 $\left(\frac{1}{\text{III}}\right)$.

DIPLOPODA. Non det. 11 $\left(\frac{1}{\text{V}}\right)$. *Ophiodesmus albonatus* (Latzel). 11 $\left(\frac{1}{\text{IV}}\right)$; sp. 11 $\left(\frac{4}{\text{I, III}}, \frac{3}{\text{I}}\right)$. Blaniulidae. Sp. 6 $\left(\frac{2}{\text{II, III}}\right)$.

ARACHNIDA. Araneida. Sp. 11 $\left(\frac{1}{\text{I}}\right)$.

Acarina. Sp. 11 $\left(\frac{1}{\text{III}}\right)$.

OLIGOCHAETA (Limicolae). 11, 1, 2, 5, 6, 11 $\left(\frac{27}{\text{I–V}}, \frac{12}{\text{III}}\right)$.

Plot No. O 1. *Dung only.*

Samples taken during months 3, 4, 5, 6, 10.

INSECTA.

Collembola. Non det. 6 $\left(\frac{1}{\text{V}}\right)$. *Anurida granaria* (Nic.) Tullb. 4, 5, 6, 10 $\left(\frac{50}{\text{I–V}}, \frac{18}{\text{III}}\right)$; *Onychiurus fimetarius* (L.) 3, 4, 5, 6, 10 $\left(\frac{26}{\text{I–V}}, \frac{11}{\text{II}}\right)$; *O. ambulans* (L.) 6 $\left(\frac{2}{\text{IV, V}}\right)$; *Achorutes purpurescens* Lubb. 3, 4, 5, 6 $\left(\frac{11}{\text{I–IV}}, \frac{5}{\text{III}}\right)$; *Folsomia fimetaria* (L.) 5 $\left(\frac{2}{\text{II, III}}\right)$; *Isotoma* sp. 4, 5 $\left(\frac{3}{\text{II, III}}, \frac{2}{\text{II}}\right)$; *Isotomurus palustris* (Mull.) 6, 10 $\left(\frac{6}{\text{I}}\right)$; *Heteromurus nitidus* (Templ.) 10 $\left(\frac{1}{\text{I}}\right)$.

Orthoptera. *Forficula auricularia* L. (nymph) 10 $\left(\frac{1}{\text{III}}\right)$.

Thysanoptera. Sp. 5 $\left(\frac{1}{\text{II}}\right)$.

Coleoptera. Carabidae. Larvae 3, 4, 5 $\left(\frac{9}{\text{I, III, V}}, \frac{4}{\text{III}}\right)$. Staphylinidae *Atheta* (*Meotica*) *exilis* Er. 4, 10 $\left(\frac{5}{\text{I, II}}, \frac{3}{\text{II}}\right)$; *Tachyporus hypnorum* F. 5 $\left(\frac{1}{\text{I}}\right)$. Larvae 4, 5 $\left(\frac{2}{\text{I, V}}\right)$. Cryptophagidae. *Atomaria linearis* Steph. 4, 5 $\left(\frac{3}{\text{I, V}}, \frac{2}{\text{I}}\right)$. Elateridae. *Athous* sp. (larvae) 4, 5, 6, 10 $\left(\frac{6}{\text{II–V}}, \frac{2}{\text{IV, V}}\right)$. Larva non det. 10 $\left(\frac{1}{\text{I}}\right)$.

Diptera. Cecidomyidae. Larvae 5 $\left(\frac{2}{\text{II, III}}\right)$. Chironomidae. Larvae 4, 5 $\left(\frac{5}{\text{II, III}}, \frac{4}{\text{II}}\right)$. Tipulidae. *Trichocera* sp. (larvae) 5, 10 $\left(\frac{5}{\text{I–III}}, \frac{2}{\text{II, III}}\right)$. Empidae. Larva 5 $\left(\frac{1}{\text{I}}\right)$. Phoridae. Larvae 3 $\left(\frac{2}{\text{III}}\right)$. Anthomyidae. Puparia 3, 4, 5 $\left(\frac{3}{\text{I, II}}, \frac{2}{\text{II}}\right)$ (one parasitised).

Hymenoptera. Ichneumonidae. *Phygadeuon fumator* Grav. 5 $\left(\frac{1}{II}\right)$ (reared from Anthomyid puparium).

"MYRIAPODA."

Chilopoda. Geophilidae. *Geophilus longicornis* Leach. 3, 5, 6 $\left(\frac{7}{I–IV}, \frac{5}{II}\right)$.

Diplopoda. Polydesmidae (probably mostly *Brachydesmus superus mosellanus* Verhoeff) 3, 4, 5, 6, 10 $\left(\frac{20}{I–V}, \frac{12}{I}\right)$; *Brachydesmus superus mosellanus* Verhoeff. 3, 5, 6, 10 $\left(\frac{15}{I–V}, \frac{5}{II}\right)$; *Ophiodesmus albonanus* (Latzel) 6 $\left(\frac{2}{II}\right)$. Iulidae. *Cylindroiulis londinensis* var. *caerulsocinctus* (Wood) 5, 6 $\left(\frac{8}{I–IV}, \frac{5}{II}\right)$. Blaniulidae. (Probably mostly *Blaniulus guttulatus* (Bosc.) 3, 4, 5, 6, 10 $\left(\frac{43}{I–V}, \frac{14}{III}\right)$. *Blaniulus guttulatus* (Bosc.) 3, 4, 5, 6 $\left(\frac{38}{I–IV}, \frac{11}{III}\right)$.

Symphyla. Sp. 5, 6 $\left(\frac{2}{III}\right)$.

ARACHNIDA.

Araneida. Sp. 4 $\left(\frac{1}{I}\right)$.

Acarina. 3, 4, 5, 6, 10 $\left(\frac{14}{I–V}, \frac{5}{II}\right)$.

OLIGOCHAETA (Terricolae). 3, 4, 5, 6, 10 $\left(\frac{62}{I–IV}, \frac{24}{II}\right)$.

OLIGOCHAETA (Limicolae). 3, 4, 5, 6, 10 $\left(\frac{462}{I–V}, \frac{162}{II}\right)$.

Plot No. O 2. *Dung, Superphosphate and Potash.*

Samples taken during months 3, 4, 5, 6, 10.

INSECTA.

Collembola. *Anuria granaria* (Nic.) Tullb. 3, 4, 5, 6, 10 $\left(\frac{16}{I–V}, \frac{5}{II}\right)$. *Onychiurus armatus* (Tullb.) 3, 4, 6 $\left(\frac{5}{I, III, IV}, \frac{3}{I}\right)$; *O. fimetarius* (L.) 3, 4, 5, 6, 10 $\left(\frac{50}{I–IV}, \frac{24}{II}\right)$; *O. ambulans* (L.) 4, 5 $\left(\frac{5}{I, II}, \frac{4}{II}\right)$; *Achorutes purpurescens* Lubb. 4, 5, 6 $\left(\frac{15}{I–V}, \frac{5}{I, II}\right)$; *Isotomurus palustris* (Mull.) 4 $\left(\frac{2}{II, V}\right)$; *Lepidocyrtus lanuginosus* (Gmel.) 5 $\left(\frac{3}{III}\right)$; sp. 10 $\left(\frac{1}{III}\right)$; *Bourletiella hortensis* (Fitch) 6 $\left(\frac{1}{I}\right)$.

Hemiptera. Jassidae. Sp. 10 $\left(\frac{1}{II}\right)$. Aphididae. *Geoica* sp. 10 $\left(\frac{3}{II}\right)$.

Coleoptera. Carabidae. Larvae 4, 5 $\left(\frac{2}{II, III}\right)$. Hydrophylidae. *Helophorus nubilus* F. 4 $\left(\frac{1}{II}\right)$. Staphylinidae. *Atheta* (*Meotica*) *exilis* Er. 3, 4, 5, 10 $\left(\frac{15}{I–V}, \frac{3}{II}\right)$; *Tachyusa umbratica* Er. 3 $\left(\frac{1}{I}\right)$; *Aleochara tristis* Grav. 5 $\left(\frac{1}{II}\right)$. Cryptophagidae. *Atomaria linearis* Steph. 4, 5, 6 $\left(\frac{3}{I–II}, \frac{2}{I}\right)$. Elateridae. *Athous* sp. (larvae) 3, 4, 6 $\left(\frac{3}{IV, V}, \frac{2}{IV}\right)$. Larvae non det. 10 $\left(\frac{1}{I}\right)$.

Diptera. Cecidomyidae. Larvae 5, 6 $\left(\frac{2}{I, III}\right)$. Mycetophilidae. Sp. 5 $\left(\frac{1}{II}\right)$.

Chironomidae. Larvae 5, 6 $\left(\frac{4}{\text{I, II}}\right)$. Tipulidae. Larva 3 $\left(\frac{1}{\text{III}}\right)$; *Trichocera* (larvae) 3, 10 $\left(\frac{2}{\text{I, III}}\right)$. Phoridae. Sp. 10 $\left(\frac{1}{\text{I}}\right)$.

"MYRIAPODA."

Chilopoda. Geophilidae. *Geophilus longicornis* Leach 3, 4, 5, 10 $\left(\frac{7}{\text{II–V}}, \frac{2}{\text{II, IV, V}}\right)$.

Diplopoda. Non det. 3, 10 $\left(\frac{7}{\text{IV, V}}, \frac{5}{\text{IV}}\right)$. Polydesmidae. (Probably mostly *Brachydesmus superus mosellanus* Verhoeff) 3, 4, 5, 6, 10 $\left(\frac{21}{\text{I–V}}, \frac{9}{\text{II}}\right)$; *Brachydesmus superus mosellanus* Verhoeff 3, 5 $\left(\frac{4}{\text{II}}\right)$; *Ophiodesmus albonanus* (Latzel) 3, 5 $\left(\frac{6}{\text{I}}\right)$. Iulidae *Cylindroiulus londinensis* var. *caerulcocinctus* (Wood) 4, 5, 6, 10 $\left(\frac{9}{\text{I–V}}, \frac{5}{\text{II}}\right)$. Blaniulidae. (Probably mostly *Blaniulus guttulatus* (Bosc.)) 4, 5, 6, 10 $\left(\frac{53}{\text{I–V}}, \frac{20}{\text{II}}\right)$; *Blaniulus guttulatus* (Bosc.) 3, 4, 5, 6, 10 $\left(\frac{35}{\text{II–V}}, \frac{24}{\text{III}}\right)$; *Archiboreoiulus pallidus* (Brade-Birks) 4, 6 $\left(\frac{10}{\text{II–III}}, \frac{9}{\text{III}}\right)$.

Symphyla. Sp. 3, 5 $\left(\frac{2}{\text{III, IV}}\right)$.

ARACHNIDA.

Araneida. Sp. 3, 4 $\left(\frac{2}{\text{I, III}}\right)$.

Acarina. 3, 4, 5, 10 $\left(\frac{11}{\text{I–IV}}, \frac{6}{\text{III}}\right)$.

OLIGOCHAETA (Terricolae). 3, 4, 5, 6, 10 $\left(\frac{36}{\text{I–IV}}, \frac{13}{\text{I}}\right)$.

OLIGOCHAETA (Limicolae). 3, 4, 5, 6, 10 $\left(\frac{255}{\text{I–V}}, \frac{120}{\text{III}}\right)$.

Plot No. A 1. *Dung and Ammonium Salts.*

Samples taken during months 4, 5, 8, 10.

INSECTA.

Collembola. *Anurida granaria* (Nic.) Tullb. 4, 5, 8, 10 $\left(\frac{55}{\text{I–V}}, \frac{15}{\text{IV}}\right)$; *Onychiurus armatus* (Tullb.) 4, 5, 8, 10 $\left(\frac{32}{\text{I–IV}}, \frac{16}{\text{II}}\right)$; *O. fimetarius* (L.) 4, 5, 8, 10 $\left(\frac{29}{\text{II–V}}, \frac{15}{\text{III}}\right)$; *O. ambulans* (L.) 8 $\left(\frac{1}{\text{IV}}\right)$; *Achorutes purpurescens* Lubb. 5 $\left(\frac{10}{\text{I–V}}, \frac{6}{\text{II}}\right)$; *Folsomia fimetaria* (L.) 5 $\left(\frac{1}{\text{I}}\right)$; *Isotoma grisescens* Schäff. 4 $\left(\frac{1}{\text{II}}\right)$; *Isotomurus palustris* (Mull.) 8, 10 $\left(\frac{3}{\text{I, III}}, \frac{2}{\text{I}}\right)$; *Heteromurus nitidus* (Temp.) 5 $\left(\frac{2}{\text{III, IV}}\right)$; *Lepidocyrtus sex-oculatus* (Schott) 8 $\left(\frac{1}{\text{III}}\right)$; *Bourletiella hortensis* (Fitch) 5 $\left(\frac{2}{\text{I}}\right)$.

Hemiptera. Homoptera (larva) 5 $\left(\frac{1}{\text{I}}\right)$.

Coleoptera. Carabidae. *Amara familiaris* Duft. 10 $\left(\frac{1}{\text{I}}\right)$; *Pterostichus* (larva) 4 $\left(\frac{1}{\text{III}}\right)$; larvae 4, 5 $\left(\frac{4}{\text{II, III}}, \frac{3}{\text{II}}\right)$. Staphylinidae. *Oxytelus nitidulus* Grav. 4 $\left(\frac{1}{\text{I}}\right)$; *O. tetracarinatus* Block. 5 $\left(\frac{1}{\text{III}}\right)$; *Scopaeus sulcicollis* Steph. 8 $\left(\frac{1}{\text{I}}\right)$; larvae 4, 8 $\left(\frac{11}{\text{I–III}}, \frac{7}{\text{III}}\right)$.

CRYPTOPHAGIDAE. *Atomaria linearis* Steph. 4, 5 $\left(\frac{24}{\text{I–V}}, \frac{11}{\text{I}}\right)$. ELATERIDAE. *Athous* sp. 8 $\left(\frac{2}{\text{II, V}}\right)$. Larvae non det. 8, 10 $\left(\frac{18}{\text{I, II}}, \frac{11}{\text{II}}\right)$.

Diptera. MYCETOPHILIDAE. Larva 4 $\left(\frac{1}{\text{II}}\right)$. CHIRONOMIDAE. Larva 4 $\left(\frac{1}{\text{II}}\right)$. TIPULIDAE. *Trichocera* sp. (larvae) 4, 5, 8 $\left(\frac{91}{\text{II–IV}}, \frac{66}{\text{III}}\right)$. PHORIDAE. Larvae 4 $\left(\frac{4}{\text{I, II}}\right)$. ANTHOMYIDAE. Pupa 4 $\left(\frac{1}{\text{II}}\right)$. Non det. pupa 4 $\left(\frac{1}{\text{II}}\right)$.

"MYRIAPODA."

Chilopoda. LITHOBIIDAE. *Monotarsobius dubosqui* (Brölemann) 5 $\left(\frac{1}{\text{II}}\right)$. GEOPHILIDAE. *Geophilus longicornis* Leach 5, 8, 10 $\left(\frac{11}{\text{I–V}}, \frac{6}{\text{III}}\right)$.

Diplopoda. POLYDESMIDAE. (Probably mainly *Brachydesmus superus mosellanus* Verhoeff) 4, 5, 8, 10 $\left(\frac{25}{\text{I–V}}, \frac{8}{\text{I}}\right)$; *Brachydesmus superus mosellanus* Verhoeff 5 $\left(\frac{3}{\text{IV}}\right)$; *Ophiodesmus albonanus* (Latzel) 10 $\left(\frac{1}{\text{IV}}\right)$. CRASPEDOSOMIDAE. *Polymicrodon polydesmoides* (Leach) 5 $\left(\frac{1}{\text{III}}\right)$. BLANIULIDAE. (Probably mainly *Blaniulus guttularus* (Bosc.)) 4, 5, 8, 10 $\left(\frac{15}{\text{I–V}}, \frac{7}{\text{II}}\right)$; *Blaniulus guttularus* (Bosc.) 5 $\left(\frac{5}{\text{III, V}}, \frac{3}{\text{V}}\right)$; *Archiboreoiulus pallidus* (Brade-Birks) 5 $\left(\frac{2}{\text{IV}}\right)$.

Symphyla. Sp. 4, 5, 8 $\left(\frac{3}{\text{I, II, IV}}\right)$.

ARACHNIDA.

Araneida. Sp. 8, 10 $\left(\frac{2}{\text{I}}\right)$.

Acarina. 4, 5, 8 $\left(\frac{6}{\text{II–IV}}, \frac{4}{\text{II}}\right)$.

OLIGOCHAETA (Terricolae). 4, 5, 8, 10 $\left(\frac{40}{\text{I–IV}}, \frac{16}{\text{I}}\right)$.

OLIGOCHAETA (Limicolae). 4, 5, 8, 10 $\left(\frac{260}{\text{I–V}}, \frac{105}{\text{III}}\right)$.

PULMONATA. 8, 10 $\left(\frac{2}{\text{I}}\right)$.

7. CENSUS OF THE FAUNA OF THE PLOTS EXAMINED.

(*a*) *Unmanured* (*Control*) *Plot* (*No.* O 8). The total number of Invertebrates in this plot in ten samples was 156, or 1,208,000 per acre. Of these 87, or 673,000 per acre, were Insects. In addition five eggs of *Leptohylemyia coarctata* (39,900 per acre) were found in this plot.

The numbers per acre of the more abundant groups were as follows: Collembola 379,000; Diplopoda 209,000; Coleoptera 163,000. There were three earthworms Oligochaeta (Terricolae) 23,000 per acre; four Acarina 31,000 per acre; Oligochaeta (Limicolae) 224,000 per acre, and no Chilopoda in the samples.

The number of species of Insects which occurred in the samples was about 30.

The following orders of Insects were represented in the percentages given: Collembola 58·3; Psocoptera 1·2; Thysanoptera 2·4; Hemiptera 1·2; Coleoptera 25·0; Diptera 9·5; Hymenoptera 2·4. The dominant order in number of species present was the Coleoptera with 12 species.

The most abundant species was *Onychiurus armatus* (Tullb.), which made up 42·9 per cent. of the total Insects, the next being *Achorutes purpurescens* Lubb. 7·1 per cent.

The "probable error" of the total number of Insects per acre is ± 36,000 or ± 5·3 per cent.

(*b*) *Ammonium Salts Plot* (*No.* A 8). Total number of Invertebrates in ten samples 182, or 1,410,000 per acre. Of these 129, or 999,000 per acre, were Insects. In addition a nest of 36 eggs of *Forficula auricularia* was met with, and 27 eggs of *Leptohylemyia coarctata* (209,000 per acre) were also found.

The numbers per acre of the more abundant groups were as follows: Collembola 643,000; Coleoptera 163,000; Acarina 147,000; Diplopoda 31,000; Oligochaeta (Terricolae) 15,000; and Oligochaeta (Limicolae) 341,000. No Chilopoda were found. Of the 19 Acarina found, 17 were hypopi clinging to a single *Forficula auricularia*.

The number of species of Insects which occurred in the samples was about 31.

The following orders of Insects were represented in the percentages given: Collembola 66·4; Orthoptera 2·4; Thysanoptera 2·4; Hemiptera 2·4; Coleoptera 9·6; Diptera 16·0; Hymenoptera 0·8. The dominant order in number of species present was the Coleoptera with 10 species.

The most abundant species was *Onychiurus armatus* (Tullb.), which made up 59·2 per cent. of the total Insects, the next being *Trichocera* larvae 5·6 per cent.

The "probable error" of the total number of Insects per acre is ± 191,000, or ± 19·1 per cent.

(*c*) *Superphosphate Plot* (*No.* O 5). Total number of Invertebrates in ten samples 224, or 1,734,000 per acre. Of these 184, or 1,424,000 per acre, were Insects. In addition three eggs of *Leptohylemyia coarctata* (23,000 per acre) were found.

The numbers per acre of the more important groups were as follows: Collembola 1,239,000; Coleoptera 163,000; Diplopoda 31,000; Chilopoda 8000; Acarina 8000; Oligochaeta (Limicolae) 209,000. No Oligochaeta (Terricolae) were found.

The number of species of Insects which occurred in the samples was about 27.

The following orders of Insects were represented in the percentages given: Collembola 87·4; Lepidoptera 0·5; Coleoptera 6·6; Diptera 3·3; Hymenoptera 1·1. The dominant order in number of species present was the Coleoptera with 9 species.

The most abundant species was *Onychiurus armatus* (Tullb.), which made up 77·0 per cent. of the total Insects, the next being *Achorutes purpurescens* Lubb. 4·9 per cent.

The "probable error" of the total number of Insects per acre is ± 285,000, or ± 20·0 per cent.

(*d*) *Dung Plot* (*No.* O 1). Total number of Invertebrates in five samples 836, or 12,948,000 per acre. Of these 150, or 2,323,000 per acre, were Insects.

The numbers per acre of the more abundant groups were as follows: Collembola 1,580,000; Coleoptera 418,000; Diptera 294,000; Oligochaeta (Limicolae) 7,155,000; Diplopoda 1,982,000; Oligochaeta (Terricolae) 960,000; Acarina 217,000; Chilopoda 108,000.

The number of species of Insects which occurred in the samples was about 25.

The following orders of Insects were represented in the percentages given: Collembola 68·0; Orthoptera 0·67; Thysanoptera 0·67; Coleoptera 18·0; Diptera 12·0; Hymenoptera 0·67. The dominant order in number of species present was the Collembola with 9 species.

The most abundant species was *Anurida granaria* (Nic.) Tullb., which made up 33·78 per cent. of the total Insects, the next being *Onychiurus fimetarius* (L.) 17·5 per cent.

The "probable error" of the total number of Insects per acre is ± 286,000, or ± 12·4 per cent.

(*e*) *Dung, Superphosphate and Potash Plot* (*No.* O 2). Total number of Invertebrates in five samples 610, or 9,448,000 per acre. Of these 143, or 2,215,000 per acre, were Insects.

The numbers per acre of the more abundant groups were as follows: Collembola 1,564,000; Coleoptera 449,000; Diptera 170,000; Oligochaeta (Limicolae) 3,949,000; Diplopoda 2,246,000; Oligochaeta (Terricolae) 558,000; Acarina 170,000; Chilopoda 108,000. Of the 11 Acarina found, three were hypopi clinging to a Diplopod.

The number of species of Insects which occurred in the samples was about 27.

The following orders of Insects were represented in the percentages given: Collembola 70·63; Hemiptera 1·40; Coleoptera 20·28; Diptera 7·69. The dominant order in number of species present was the Collembola with 10 species.

The most abundant species was *Onychiurus fimetarius* (L.), which made up 34·48 per cent. of the total Insects, the next being *Achorutes purpurescens* Lubb. 12·41 per cent., *Anurida granaria* (Nic.) Tullb. 11·03 per cent., and *Atheta* (*Meotica*) *exilis* Er. 10·34 per cent.

The "probable error" of the total number of Insects per acre is ± 303,000, or ± 13·5 per cent.

(*f*) *Dung and Ammonium Salts Plot* (*No.* A 1). Total number of Invertebrates in five samples 679, or 10,516,000 per acre. Of these 302, or 4,677,000 per acre, were Insects.

The numbers per acre of the more abundant groups were as follows: Collembola 2,037,000; Diptera 1,533,000; Coleoptera 991,000; Oligochaeta (Limicolae) 4,027,000; Diplopoda 790,000; Oligochaeta (Terricolae) 620,000; Chilopoda 185,000, Acarina 93,000. Of the 99 Diptera found, 91 were larvae of *Trichocera*, which occurred in one sample.

The number of species of Insects which occurred in the samples was about 29.

The following orders of insects were represented in the percentages given: Collembola 45·70; Hemiptera 0·33; Coleoptera 21·19; Diptera 32·78. The dominant order in number of species present was the Collembola with 12 species.

The most abundant species was *Trichocera* sp. (larvae), which made up 30·23 per cent. of the total Insects, the next being *Anurida granaria* (Nic.) Lubb. 18·27 per cent. or, excluding *Trichocera* larvae, 26·19 per cent.

The "probable error" of the total number of Insects per acre is ± 1,180,000, or ± 25·0 per cent.

For the undunged plots taken together the total fauna is 1,451,000 per acre, of which 1,032,000 are Insects. The "probable error" on this total number of Insects is ± 182,000 or ± 12·5 per cent.

Taking the dunged plots together the total fauna is 10,971,000 per acre, of which 3,072,000 are insects. The "probable error" on this total number of insects is ± 351,000 or ± 11·36 per cent.

8. Comparison of the Fauna of the Plots.

In comparing the populations of the different plots, much the most striking difference appears to be between the three not manured with dung, and the three to which dung is applied, irrespective of their treatment as regards artificial manures. The populations per acre of the separate plots and of the undunged and dunged plots considered together, are tabulated in Table I and are also shown diagrammatically in Figs. 1 and 2. The differences in the figures for total Insects are not

Table I.

Number of individuals in the different orders of Insects and other groups in the various plots.

Thousands per acre.

	Separate plots						Averages	
	O 8	A 8	O 5	O 1	O 2	A 1	Undunged	Dunged
Collembola	379	643	1239	1580	1564	2037	754	1727
Orthoptera	—	23	—	15	—	—	8	5
Psocoptera	8	—	—	—	—	—	3	—
Thysanoptera	15	23	8	15	—	—	15	5
Hemiptera	8	23	8	—	31	15	13	15
Lepidoptera	—	—	8	—	—	—	3	—
Coleoptera	163	163	163	418	449	991	163	620
Diptera	62	155	46	279	170	1533	88	661
Hymenoptera	15	8	15	15	—	—	13	5
Total Insects	673	999	1424	2323	2215	4677	1032	3072
Chilopoda	—	—	8	108	108	185	3	134
Diplopoda	209	31	31	1982	2246	790	90	1673
Symphyla	8	—	—	31	31	46	3	36
Araneida	23	8	8	15	31	31	13	26
Acarina	31	147	8	217	170	93	62	160
Oligochaeta (Terricolae)	23	15	—	960	558	620	13	712
Oligochaeta (Limicolae)	224	341	209	7155	3949	4027	258	5044
Isopoda	15	—	—	—	—	—	5	—
Pulmonata	—	—	—	—	—	31	—	10
Total fauna	1208	1410	1734	12,948	9448	10,516	1451	10,971

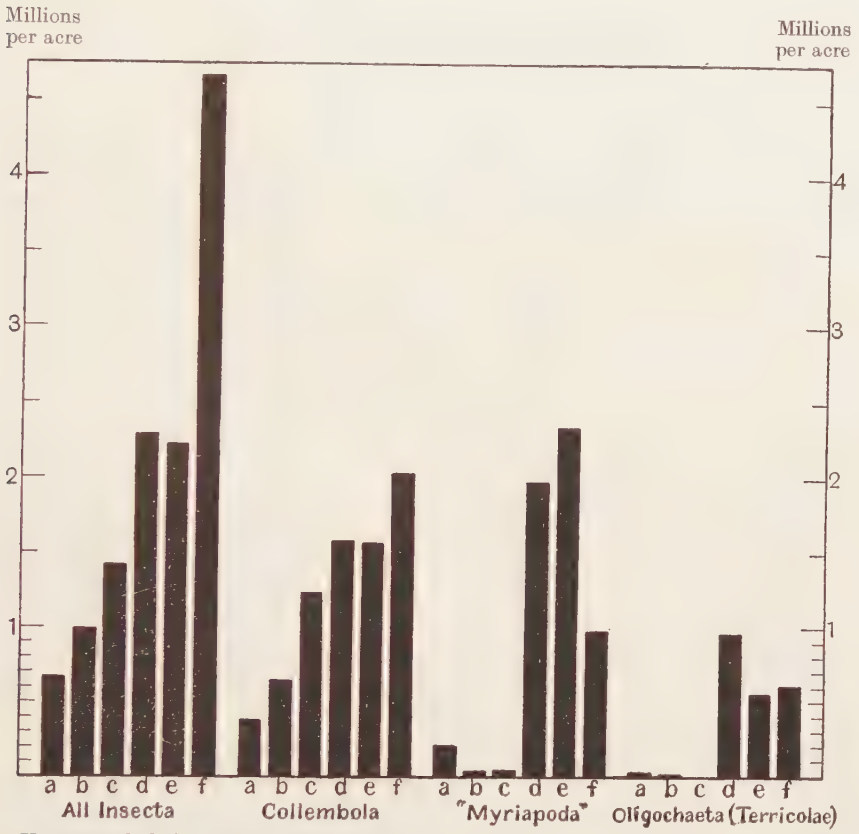
Table II.

Number of species in the different orders in the various plots.

	Plots						Averages	
	O 8	A 8	O 5	O 1	O 2	A 1	Undunged	Dunged
Collembola	6	7	7	9	10	12	6·6	10·3
Orthoptera	—	2	—	1	—	—	·6	·3
Psocoptera	1	—	—	—	—	—	·3	—
Thysanoptera	1	1	1	1	—	—	1·0	·3
Hemiptera	1	2	1	—	2	1	1·3	1·0
Lepidoptera	—	—	1	—	—	—	·3	—
Coleoptera	10	10	9	7	9	10	9·6	8·6
Diptera	7	7	5	6	6	6	6·3	6·0
Hymenoptera	2	1	2	—	—	—	1·6	—
Chilopoda	—	—	—	1	1	2	—	1·3
Diplopoda	2	2	2	4	5	5	2·0	4·6

significant between the separate undunged and dunged plots, but between these groups of plots taken together the difference is distinctly significant.

This increase in number in the plots receiving dung is noticeable in all groups of Insects and other Invertebrates, as well as in the totals,



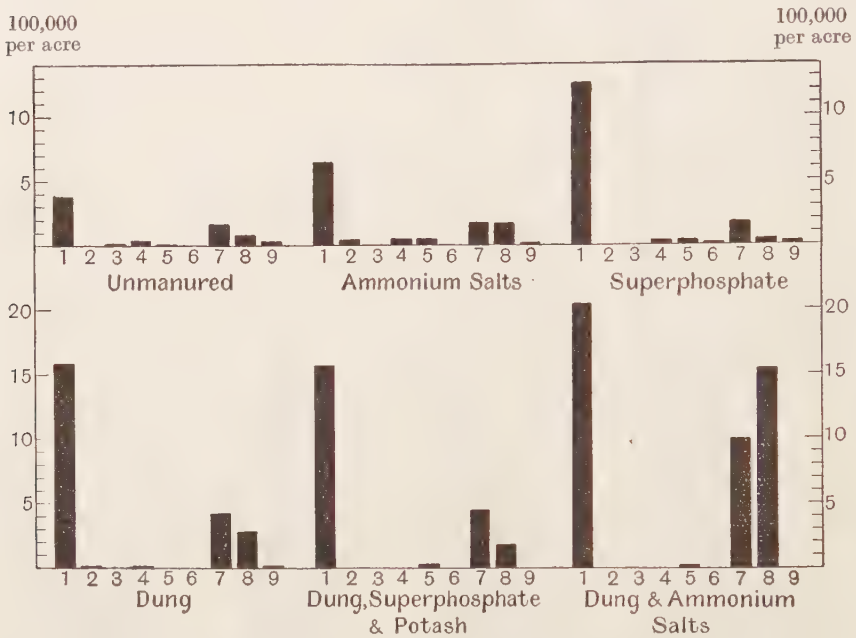
a, Unmanured; *b*, Ammonium salts; *c*, Superphosphate; *d*, Dung; *e*, Dung, superphosphate and potash; *f*, Dung and ammonium salts.

Fig. 1. Number of individuals in the more important groups in the various plots.

and the numbers of species were also increased (Table II). The increase is most marked in the case of the Oligochaeta (Limicolae) which are present in small numbers without dung, but very numerous where dung is applied. Oligochaeta (Terricolae) from being present in very small numbers without dung are numerous with it, Diplopoda are very much increased by dung, and Chilopoda and Elateridae larvae, almost absent

where dung is absent, are present in small numbers where dung is applied.

Of the species of Collembola present *Anurida granaria* and *Onychiurus fimetarius* are much more abundant in the presence of dung, becoming the most abundant species; in the undunged plots *Onychiurus armatus* is much the most abundant species, and is present in considerably greater numbers than it is in the dunged plots. This is the only case observed in which a species was more plentiful in the absence of dung.



1, Collembola; 2, Orthoptera; 3, Psocoptera; 4, Thysanoptera; 5, Hemiptera; 6, Lepidoptera; 7, Coleoptera; 8, Diptera; 9, Hymenoptera.

Fig. 2. Number of individuals in the different orders of insects in the various plots.

It is noteworthy also that the injurious Diplopoda were much increased by the application of dung and that Elateridae larvae were also increased.

The occurrence during both autumns over which the investigation extended of eggs of *Leptohylemyia coarctata* is of considerable interest, and has been dealt with more fully elsewhere (7). The larvae of this fly may have been living in the plants of couch grass (*Triticum repens*) which occur in the field, although no such larvae were observed in the few plants of this grass which were examined. Adults of *Atomaria*

linearis were the most plentiful Coleopteron and were more numerous in the plots receiving dung, and particularly so in the plot A 1 receiving dung and ammonium salts. This species is known to be a pest of mangolds and in some years has caused considerable damage to the crop in this field. The larva of this species was not recognised, but some unidentified larvae which occurred may have been those of this species.

In connection with the Elateridae larvae it may be mentioned that all the specimens obtained, except one, belonged to the genus *Athous*, while a considerable number obtained from a permanent pasture field adjoining and separated only by a fence, all belonged to the genus *Agriotes*, although there has not apparently been any previous suggestion of either having any particular preference for one type of land rather than another.

9. Distribution in Depth.

The samples of soil were taken, as was done previously, in five layers, so that the depth at which the specimens occurred could be recorded. These five layers were, as before: I, surface to one inch below the lowest point of the surface; II, one to three inches; III, three to five inches; IV, five to seven inches; V, seven to nine inches. In taking a sample it was usually quite evident that ploughing had affected the soil to a depth of about five or six inches, a distinct change in the appearance of the soil being noticeable in layer IV, between five and seven inches.

The distribution in depths of the groups—All Insecta, Collembola only, "Myriapoda" and Oligochaeta (Terricolae)—is shown in the diagram (Fig. 3). As was found in the previous investigation, most Insecta and Oligochaeta (Terricolae) were found in the upper five inches of the soil, although the preference for the second level, at a depth of one to three inches, was not so marked, and in several cases most individuals were found in the layer between three to five inches deep.

In some groups, no individuals were found at a greater depth than seven inches, although from the diagram it seems probable that the Insects, Collembola, and "Myriapoda" occur to a greater depth than nine inches, at least in the plots receiving dung.

The percentages of the total Insects at the different depths were:

Unmanured plot:	I 28·0; II 33·6; III 15·7; IV 16·1; V 6·7.
Ammonium salts:	I 19·0; II 45·7; III 21·3; IV 9·3; V 4·7.
Superphosphate:	I 14·1; II 32·9; III 36·0; IV 13·0; V 4·0.
Dung:	I 22·8; II 28·2; III 30·9; IV 9·4; V 8·5.

Dung, superphosphate and potash: I 17·2; II 41·0; III 22·1; IV 11·0; V 8·2.

Dung and ammonium salts: I 18·1; II 23·7; III 35·8; IV 14·1; V 8·2.

Owing to the samples from the undunged plots having been taken only during the winter and those from the dunged plots only during the summer, no seasonal variation in distribution is observable, nor is it possible to observe any variation in distribution due to ploughing, as the ploughing was done during the period that samples were being taken from the undunged plots, and the numbers of Insects obtained in each sample from these plots was too small for a useful comparison.

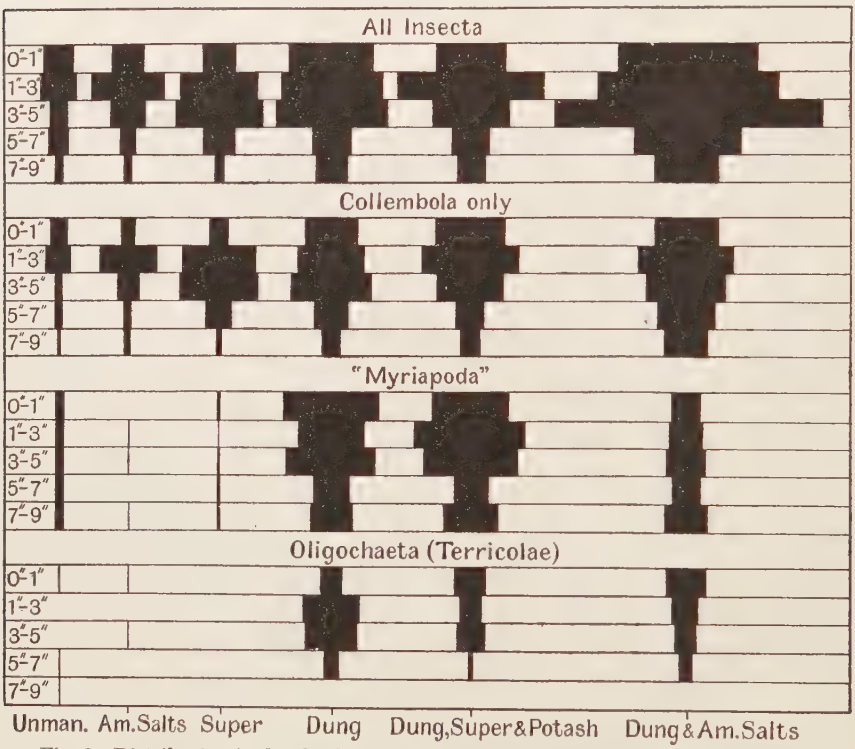


Fig. 3. Distribution in depth of the more important groups in the various plots.

10. Comparison with other Soil Fauna of Arable Land.

Comparing the insect population of the plots at present under consideration with that of the plots examined previously in Broadbalk field (6), it is at once apparent that the number of Insects present is much

smaller in the present instance. The population of the plots not receiving dung is, in Barn Field, between 500,000 and 1,500,000, as compared with nearly 2,500,000 in the unmanured plot of Broadbalk, the completely unmanured plot of Barn Field containing under 700,000 Insects per acre.

In the case of the dunged plots of Barn Field, the population of two was about 2,250,000 per acre, and of the third 4,750,000, the larger number obtained from the latter plot being due, however, to one unusually rich sample. In Broadbalk the number of insects in the dunged plot was about 7,750,000, so that the numbers of insects in the dunged plots of Barn Field are nearer to that of the unmanured plot of Broadbalk.

The following definitely determined species of Insects were found in Barn Field, which had also been found in Broadbalk:

Onychiurus fimetarius, *O. ambulans*, *Isotoma minor*, *Isotomurus palustris*, *Orchesella villosa*, *Heteromurus nitidus*, *Lepidocyrtus cyaneus*, *Forficula auricularia*, *Helophorus nubilus*, *Stenus subaenus*, *Oxytelus tetracarinatus*, *O. inustus*, *O. nitidulus*, and *Tachyporus hypnorum*.

It is probable that some of the larvae of Coleoptera and Diptera which were not specifically identified were also smaller.

Amongst the "Myriapoda" the following species are common to both fields: *Brachydesmus superus mosellanus*; *Cylindroiulus londinensis* var. *caeruleocinctus*; *Blaniulus guttulatus*; *Archiboreoiulus pallidus*, and *Geophilus longicornis*.

The most interesting new species occurring in Barn Field are *Anurida granaria* and *Onychiurus armatus* which occur in considerable numbers in the dunged and undunged plots respectively. The two species *Atomaria linearis* and *Bourletiella hortensis* are also of interest as they are both pests of mangolds, and the latter caused considerable damage to the young mangold plants during 1926, and, for a short time, was present in very large numbers.

Probably the cause of the differences in soil population between the dunged and undunged plots of Barn Field and those of Broadbalk is the very different amount of cover provided in the two cases by the crop and weeds, and the very different proportions of the year that the fields are bare. In the case of Broadbalk, on which wheat is grown every year, on the dunged plot the crop provides abundant cover through the spring and summer, and in addition to the wheat plants, weeds are present in abundance, and the only cultural operation possible during this time is hand hoeing, which does not cause any very great disturbance of the soil. The only period of the year during which ploughing, etc.,

can be carried out is between the harvest and the autumn drilling for the next year's crop, a period of a month or two. On the unmanured plot of Broadbalk the growth of the crop is not nearly so thick and weeds are less abundant than on the dunged plot, so that not nearly so much cover is provided.

On Barn Field, on which mangolds are grown every year, the crop does not provide more than very scanty cover until well into the summer, and, although weeds are fairly abundant here also, there is nothing approaching the tangle of vegetation which occurs on the dunged plot of Broadbalk. Cultural operations are possible on Barn Field from about November until the next year's crop is sown, about the end of April, and, during most of the summer, hoeing—both by horse and by hand —is carried out at intervals.

From the foregoing comparisons it appears that the soil fauna is influenced largely by the use of dung as manure, and by the amount of vegetation on the ground, and to a very small extent, if at all, by the use of artificial manures.

Since the previous paper by the present writer was published in 1922, an important paper on the soil fauna near Aberystwyth by Miss M. Thompson (9) has been published. In this paper the author gives an account of an investigation of the soil fauna of pasture land, ungrazed grassland, land recently ploughed, and of cultivated land, of which the latter is most nearly comparable with the area discussed in the present paper, although the manuring and cropping have not been the same from year to year, the field thus being more typical of normal arable land than Barn Field. This irregularity of treatment has probably prevented the manuring from having any marked effect.

The numbers per acre calculated from Miss Thompson's data give about 4,500,000 Insects per acre, of which over 94 per cent. were Collembola. This total is greater than that in two of the three dunged plots examined in Barn Field but the number of Insects other than Collembola is not so great at Aberystwyth as in the dunged plots of Barn Field, probably owing to the heavy and regular dressings of dung on the Barn Field plots: the number of Insects other than Collembola at Aberystwyth is not greatly in excess of the numbers in the undunged plots of Barn Field. Possibly the much greater numbers of Collembola at Aberystwyth may be due to the open and porous nature of the soil there, compared with the high percentage of clay in the Barn Field.

The number of Oligochaeta which would come under the grouping "Oligochaeta (Terricolae)" used in the present paper, is rather less at

Aberystwyth than in the dunged plots of Barn Field, and of the group "Oligochaeta (Limicolae)" is very considerably less. This again is directly attributable to the much smaller amount of dung the ground there had received.

The Diplopoda, while more numerous in the Aberystwyth area than in the Barn Field undunged plots, are considerably less numerous than in the dunged plots; even on an occasion when they were causing appreciable damage at Aberystwyth their number was less than their average number on two of the dunged plots.

Summary.

Samples of soil were taken from six of the plots of Barn Field on the farm of the Rothamsted Experimental Station, and the Insects and other Invertebrates found therein are recorded together with the approximate depth at which they occurred.

On these plots one receives no manure, one superphosphate only and one ammonium salts only, while of the other three, all of which receive dung, one receives superphosphate and potash, and another ammonium salts in addition.

The total number of Insects and other Invertebrates per acre in the undunged plots were 1,208,000, 1,410,000 and 1,734,000 respectively. Of these 673,000, 999,000 and 1,424,000 respectively were Insects. Similarly in the dunged plots the total numbers of Insects and other Invertebrates per acre were 12,948,000, 9,448,000 and 10,516,000 respectively, and of these 2,323,000, 2,215,000 and 4,677,000 respectively were Insects.

Each sample was taken in five layers so that it was possible to record the approximate depth at which each individual occurred. The greatest number, both of Insects and of other Invertebrates, occurred in the upper five inches of the soil.

From the figures obtained in this investigation it appears that artificial manures have little or no effect on the soil fauna, while the effect of dung in increasing the numbers and the number of species of the fauna is very considerable.

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(*Received* 23*rd March*, 1927.)

NOTE ON THE ACTIVITIES OF HUMBLE BEES (*BOMBUS*) IN NORTH WALES

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In August 1923 the writer published a short article in the *Entomologists' Monthly Magazine* giving a brief account of the activities of various species of Bombi noted during the period 1913–21, chiefly from records gathered in North Wales in 1919–21, together with a few from Mid-Wales, and other parts of the west of England. These notes have since been extended (1923–26) by a further mass of records from North Wales (and a few from West Herefordshire and Montgomeryshire).

As a result it is believed that a fairly complete idea has been gained of the work of the more abundant species, throughout their active periods, at any rate for North Wales, and adjacent regions. The less abundant mountain species have received less attention than the more abundant lowland forms. To tabulate the full activities of each species would require more space than seems commensurate with the subject and an attempt is made to combine the chief information as far as possible in one table. The data presented was gathered, for the most part during field work in ordinary agricultural land, gardens, etc., and no type of cultivation was given predominance.

All records relate to actual flower visits, including the dates given for "First noted" and "Last noted," which do not refer to nest-hunting "queens," etc.

The following species have been noted during the work, and are given below together with some general remarks, and a list of the flowers visited (other than those of chief economic value, which will be found in the table appended). The records are not given in botanical order but in sequence of seasonal observation.

(1) BOMBUS LAPIDARIUS. Common everywhere. Recorded from a total of 27 flower species (economic and non-economic). Gorse, Rosemary, Rhododendron, Garden Anemone, Dog Violet, Apple, Daisy, Bluebell, Buttercup, Laburnum, Escallonia, *Vicia sepium*, Self Heal, Yellow Rattle, *Centaurea nigra*, Hieracium, Wild Thyme, *Leontodon autumnale*, Rest-harrow, Red Bartsia, various meadow Compositae, Brassicas.

(2) B. TERRESTRIS and (3) B. LUCORUM. These two species are both very abundant, and in their times of appearance and activities show great similarity. *B. terrestris* has been recorded from 45 flower species, and *B. lucorum* from 54.

The flowers visited by the latter include Rosemary, Heaths (Garden), *Berberis* spp., Mahonia, Gorse, Dandelion, Red Ribes, Sallows, Bluebell, Sycamore, Ground Ivy, Iris, Escallonia, Charlock, Lousewort, Ox-eye Daisy, Sage (Garden), Caper Spurge, Sheep's Scabious, Fuchsia, *Hieracium* spp., *Helianthemum* sp., *Campanula* spp., Burdock, Figwort, Thistles, Bartsia, Snowberry, Scabious, Privet, Wood Sage, *Solanum jasminoides*.

(4) B. SORRÖENSIS. Recorded in small numbers, July to September, on Dandelions, Blackberry, and *Centaurea scabiosa*.

(5) B. PRATORUM. Common in North Wales, and recorded as visiting 36 species of flowers, the non-economic species being Berberis spp., Wood Anemone, False Strawberry, Heaths, Dandelion, Bluebell, Laburnum, Columbine, Marigold, Comfrey, Yellow-Rattle, Escallonia, Snowberry, Thistles, *Hypericum* sp., Sheep's Scabious, Veronica (cultivated), Rest-harrow, Antirrhinum, *Cotyledon umbilicus*, Charlock, Sea Holly, *Centaurea nigra*.

(6) B. JONELLUS. A rare mountain species in North Wales, a few having been obtained from June to August on *Jasione montana*, *Erica cinerea*, and *E. vagans*.

(7) B. LAPPONICUS. Not a common species. Recorded from May 27th to end of August, visiting *Cardamine pratensis*, White clover, *Pedicularis sylvatica* (once each) and fairly common on Blackberry and *E. vagans*.

(8) B. RUDERATUS. The only specimens referable to this species are several melanic ♂♂ collected about Dyserth and Rhyl, August 10th, 1923. These were entirely black with the exception that "the beards of the mandibles are rust-coloured" as stated by Sladen (2), p. 175, also a few pale hairs and a tendency to greyish-brown on the tail, more especially beneath. No females or workers were obtained although sought for.

(9) B. HORTORUM. Common, and reported from 23 flower species. Primrose, Pulmonaria, Bluebell, Columbine, Hawthorn, Escallonia, Red Campion, Horse-Chestnut, Sage (Garden), *Convolvulus major*, Foxglove, *Centaurea nigra*, Self-Heal, *Stachys germanica*, *S. sylvatica*, Wood Sage, Antirrhinum (Garden), Burdock, Fuchsia, Honeysuckle, Bell-Heather, Herb-Robert Thistles, *Tropaeolum indicum*, Common Hemp Nettle.

(10) B. DISTINGUENDUS. A fine "queen" was taken near Bangor, June 22nd, 1924, crawling on a road, during cold, windy weather.

(11) B. LATREILLELLUS. Only one specimen was taken, July 11th, 1920, on white Clover near Bethesda.

(12) B. DERHAMELLUS. Local, recorded April–July on Dog Violets, Yellow Rattle, and *Lathyrus pratense*.

(13) B. AGRORUM. The most abundant species in North Wales, found throughout the season, and later than any other species, being noted as visiting *Galeopsis* near Bethesda at 700 feet on November 18th, 1926. Collected from 70 flower species, including Herb Robert, Wallflower, Dog Violets, Dandelions, Ground Ivy, Lungwort, Bilberry, Garden Brassicas, Lady's Smock, *Lathyrus* sp., *Valeriana pyrenaica Centaurea* sp., Comfrey, *Ajuga reptans*, Purple Dead-nettle, Blue-bell, Lesser Spearwort, Dog Rose, Garden Roses, (White) Rhododendrons, Escallonia, Horse-Chestnut,

Mimulus sp., Sage (Garden), Foxglove, Red Campion, *Vicia cracca*, *Lotus major*, Shirley Poppy, Sheep's Scabious, Burdock, Spear Thistle, *Calamintha*, Hemp Nettle, Wood Sage, Self Heal, Wood Betony, Antirrhinum (Garden), Purple Loose-strife, Fuchsia, *Vicia orobus*, Gorse, Field Scabious, *Stachys sylvatica*, Red Bartsia, White Dead-nettle, Hollyhock.

(14) B. HELFERANUS. Local, and appears late, not being recorded prior to July 16th. In addition to a few economic records (see Table) it has occurred on Hollyhock and *Centaurea nigra*.

(15) B. MUSCORUM. Only one definite record, a queen taken by Mr W. Maldwyn Davies, B.Sc. This specimen was pollen-collecting on Lilies, Bangor, June 18th, 1924.

In the table the following abbreviations are used:

c. = common; v.c. = very common; f.c. = fairly common; s. = several records in different years.

(*1*), (*2*), etc., indicate only that number of records.

The other figures denote months.

General Notes.

In 1923 the spring weather was cold, with practically no early bursts of heat and very few ♀♀ Bombi were noted until the warm days of May 7th–10th, when great numbers were seen. In marked contrast was April 9th, 1926, when "queens" of six species were abundant and active.

A ♂ and ♀ of *B. hortorum* were collected in copula on herbage on the headland of a field of mangolds, etc., at 2 p.m. on Sept. 10th, 1926, in bright hot weather, in Carnarvon.

As regards "robbing" the only two instances noted both relate to *B. pratorum*, the first of workers nectar sucking from numerous perforated flowers of Comfrey, at Aber, May 11th, 1926, and the second at Bangor, June 13th, 1926, when the flowers of Broad Beans were being visited at 9.30 p.m. (summer time). In this case the bases of all the corollas were badly damaged by perforations made on their upper surface. In neither instance was *pratorum* observed actually doing the damage.

B. pratorum was likewise observed nectar sucking from the extra floral nectaries of Broad Beans, in a Bangor garden, June, 1926. Williams (3) dealing with red clover at Aberystwyth concluded that not more than 4–5 per cent. of the total bees present were "robbers."

B. hortorum was observed visiting and nectar sucking from "thrum" eyed flowers of Primrose in April, 15 being visited in rapid succession on two contiguous roots growing on a rockery amongst many other plants.

Further instances noted of bees passing from one flower species to another are as follows: (1) *B. lapidarius* ♀, *Bellis perennis* to *Viola* sp. (dark blue). (2) *B. hortorum* (at 1000 ft. in Montgomeryshire), Foxglove

Table showing work of Bombi.

Species of Bee	Fruit, Crops and Vegetables																Remarks
	Apple	Pear	Plum	Cherry	Rasp-berry	Black-berry	Goose-berry	Currant	White Clover	Red Clover	Alsike	Lotus	Broad Bean	Runner Vetch	Runner Bean	Runner Marrow	
B. lapidarius	4 s.	—	—	—	—	7–8 f.c.	—	—	6–7 f.c.	5 s.	—	6–8 s.	—	6	—	—	Common everywhere. First noted Apr. 6th. Last noted Sept. 2nd. Most abundant June–Aug.
B. terrestris	4–5 f.c.	5	4 c.	4 c.	6 c.	7 c.	4 f.c.	4 s.	6	6–7 (*1*)	7	—	6–7	8 v.c.	7–8 c.	9 s.	Common everywhere. First noted Apr. 1st. Last noted Sept. 10th. Most abundant Apr.–Aug.
B. lucorum	5–6 f.c.	—	4 f.c.	4	5–6 c.	7 c.	4 s.	4–5	6–7–8 f.c.–s.	6	6–7 c.	6	6–7 v.c.–s.	8 v.c.	7–8	9 s.	Common everywhere. First noted Apr. 1st. Last noted Sept. 25th. Most abundant Apr.–Aug.
B. pratorum	5 s.	—	4 s.	4 (*1*)	5–6 c.	6–7	3 (*1*)	5 s	—	—	—	7	—	—	6	—	First noted Apr. 1st. Last noted Aug. 17th. Most abundant Apr.–July.
B. hortorum	—	—	—	—	7 c.	7 c.	—	—	7 s.	7 s.	—	—	6 f.c.	—	—	9	First noted Apr. 25th. Last noted Oct. 14th. Most abundant June–July.
B. agrorum	4–5	—	4 (*1*)	—	5 f.c.	6–7–8 c.	—	—	6–7	6–9 c.	6–7 v.c.	6–7 v.c.–(*1*)	6 f.c.	7	7 c.	9	Very abundant. First noted Apr. 6th. Last noted Nov. 10th. Most abundant May–Sept.
B. derhamellus	—	—	—	—	5	—	—	—	7	7	—	—	—	—	—	—	Local. Apr.–Aug.
B. helferanus	—	—	—	—	—	8 s.	—	—	7	9 (*1*)	—	—	—	—	—	—	Local. July 16th–Sept. 24th.

to *Stachys sylvatica* (several) and on to *Erica cinerea*. (3) *B. agrorum*, worker, *C. nigra* to *Hierachium* sp. This species was also observed to visit colonies of *Psylla crataegi* on Hawthorn, near Bangor, June, 1926, in order to lap up "honey dew."

Summary.

1. A short account is given of the species of Humble Bees (Bombi) observed by the writer in North Wales and adjacent districts during the period 1919–27, with notes on their relative abundance and seasonal activities.

2. The chief economic plants visited by each species are listed, together with brief mention of those cultivated and wild flowers most favoured.

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(*Received 14th May*, 1927.)

ON THE PAIR OF SO-CALLED SENSORY PITS OF THE NINTH ABDOMINAL SEGMENT OF THE WIREWORM (*AGRIOTES OBSCURUS* LIN.) WITH ADDITIONAL NOTES ON THE INTERNAL ANATOMY

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(With 9 Text-figures.)

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1. Introduction.

This paper represents an endeavour to ascertain the structure and the function of the curious pair of stigma-like depressions or pits (Fig. 1, *PT*) which are to be found on the ninth abdominal segment of the wireworm (*Agriotes obscurus* Lin.). Earlier writers erroneously referred to them as spiracles but later authors have described them either as muscular impressions or sensory pits.

Horst(6), 1922, suggests that they may represent a modified ninth pair of stigmata and points out that nowhere in the literature is he able to obtain any guidance concerning the significance and embryological development of these structures.

Whilst examining the voluminous literature which has accumulated concerning such an important economic species as the wireworm the writer was rather surprised to note that practically nothing has been recorded concerning the internal anatomy of the wireworm nor indeed of Elaterid larvae generally.

For instance, Horst (6) in his fairly elaborate paper on the morphology and biology of the Elateridae gives no account of the internal anatomy of the larvae, although the external appearance is extensively treated. Consequently some additional information has been included in this paper on the internal anatomy of *Agriotes obscurus* (larva).

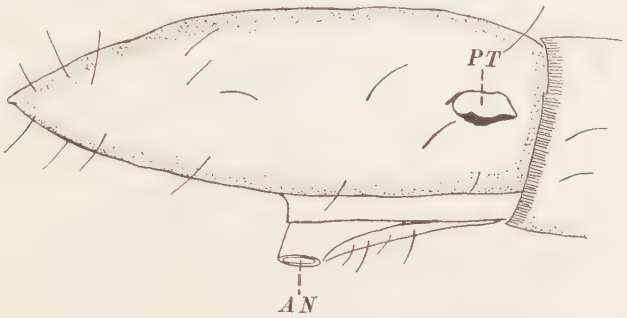

Fig. 1. The lateral view of the last or ninth abdominal segment of the larva of *Agriotes obscurus*. ×50. *AN*, anus; *PT*, pit.

I desire to thank Prof. J. S. Gardiner, F.R.S., for the facilities he has afforded me to carry out this work in his laboratory.

Acknowledgements are due to Mr A. Rymer Roberts, M.A., who determined the instars of some of the wireworms worked on; to Dr Keilin, who examined my sections of the malpighian tubes; and also to Mr F. R. Petherbridge, of the School of Agriculture, Cambridge, who provided me with some material.

2. Technique.

The chief technical difficulty encountered in attempting to obtain sections through the region of the pits or indeed through any part of a wireworm is the well-known toughness and thickness of the cuticle.

The following method was devised to obtain sections through the pits.

The larvae were fixed in either Carnoy's (No. 2 formula) or Bouin's fluid and the ninth abdominal segment then cut away and embedded in paraffin wax using ordinary methods. The embedded segment was then cut out of the wax and the two parts of the segment containing pits cut away, care being taken to chip away as much of the integument as possible without injuring the pits and the soft structures associated with them. The chitinous wall of the pits is much thinner than that of the cuticle of the general body surface and after being re-embedded good

sections were obtained. Whole mounts were also made of the pits and nitric acid proved a useful and rapid decoloriser of the chitinous parts.

For the examination of the internal anatomy of the larva dissections were made and the parts studied were both mounted whole and sectioned. The alimentary canal and associated structures were best cut at 6 μ thick but the best sections of the chitinous parts were obtained from

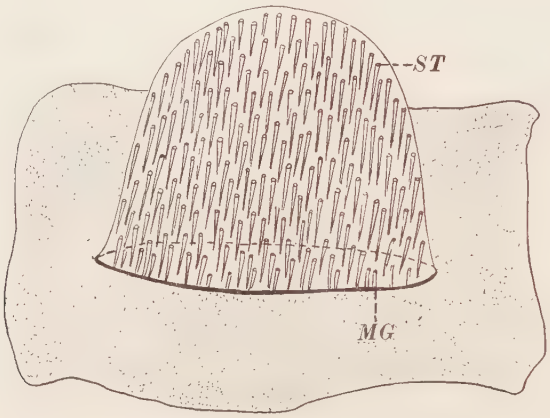

Fig. 2. One of the pits on the last abdominal segment of *A. obscurus* (larva) viewed from the inner aspect and rendered partly transparent with nitric acid. ×630 diams. *MG*, thickened margin of pit; *ST*, setae lining the outer surface of the pit wall.

sections 10 μ thick. Delafield's iron haematoxylin proved sufficient for nearly all staining purposes and safranin was occasionally used as a counter stain.

All sections and dissections were made from larvae of the last instar. I am indebted to the late Dr C. L. Withycombe for securing for me a supply of reliable indicators which were used to test the reaction of the various parts of the alimentary canal and its contents.

3. The "Sensory" Pits.

The external appearance of these two depressions or pits which are to be found on the last abdominal segment of the larva of *Agriotes obscurus* has been adequately described by Roberts (8).

This worker in describing the ninth abdominal segment of the wireworm (*A. obscurus*) writes: "The ninth abdominal segment is considerably longer than the preceding one, conically paraboloid (Beling (1)) with a pair of large open pits margined with brown situated near the anterior margin of the tergite. In life they are nearly round but contract at the

sides to an elongated oval shape when preserved in spirit. Their margin of stout brown chitin is somewhat raised above the general area of the tergite on either side. Within the pits are lined with a pale membrane which bears numberless minute dark hairs arranged over the entire surface. Similar fine hairs are also found on the inner surface of the chitinous rim just mentioned. In consequence of the presence of these hairs situated in pits the latter are presumed to have a sensory function though what it may be has not been ascertained. Formerly they were supposed to be spiracles but more recently they have been referred to as muscular impressions by Henriksen (5) and Schiodte (9).

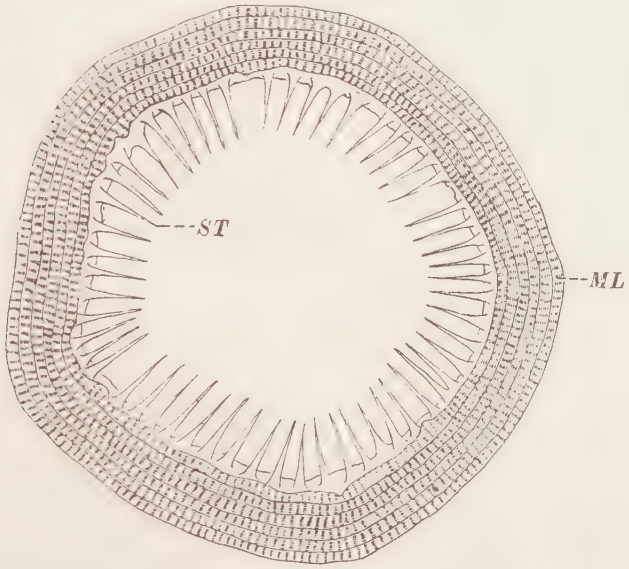

Fig. 3. A transverse section of a pit. ×780 diams. *ML*, muscles which completely surround the inner surface of the pit wall; *ST*, setae lining the outer surface of the pit wall.

An examination of sections of the pit wall show that the hairs (Figs. 2 and 3, *ST*) lining its outer surface are setiform in shape and arise from the general surface of the cuticle. Moreover, they do not possess a nervous supply at their bases and consequently cannot be differentiated from ordinary body hairs nor grouped with any known type of sensillae.

No other type of structure which is associated with sense reception in insects was found in the region of the pits and neither by dissection nor by examination of sections was any direct nerve supply traced to the pits. Lining the inner surface of the pit wall and closely appressed to it is a thick layer of muscular tissue (Fig. 3, *ML*). From the foregoing

it appears that if these pits and their setae possess any function of a sensory nature it must be of a very diffuse and unspecialised type. It is possible, keeping in view the fact that the cuticle of the pit wall is thinner than that of the general body integument, that the animal may be sensitive to differences of pressure in the region of the pit of which the greater resisting power of the rest of the cuticle would otherwise render it oblivious.

From this study of their structure, however, the term sensory pits does not seem to be justified and the evidence seems to point to the fact that they are connected in some way with the functions of the muscles and are very probably rather large muscular impressions.

In reference to the opinion of Horst(6) that the pits may represent a modified ninth pair of spiracles it may be stated that no structures were found which would tend to support such a view, but as my sections were made entirely from larvae in the last instar a study of earlier stages might prove useful.

4. The Alimentary Canal.

The alimentary canal is a practically straight tube which is remarkably free from the appendicular glands often associated with the gut of both larval and adult insects.

A very careful search enables the writer to state definitely that those structures usually referred to as salivary glands in insects are absent. This state of affairs is not an unusual occurrence in both larval and imaginal Coleoptera. Gastric coeca also are not found and histological evidence suggests (Fig. 6) that the digestive fluids are secreted entirely by the epithelial lining of the mesenteron.

Immediately behind the oral opening the gut swells slightly to form a pharynx (Fig. 4, *PH*) and thereafter narrows and is continued as the oesophagus (Fig. 4, *OE*) to about the posterior region of the second thoracic segment where the calibre of the tube again increases sharply to form the mesenteron (Fig. 4, *MS*). The inner surface of the wall of the oesophagus projects into the lumen to form four longitudinal ridges extending the whole of its length (Fig. 5, *LR*). They are supplied with muscular elements from the circular layer (Fig. 5, *CM*) and by their movements assist the passage of food along the gut.

The longitudinally arranged muscle bands are very powerful, especially in the region of the pharynx.

The oesophagus at its junction with the mesenteron projects somewhat into the lumen of the latter (Fig. 4, *EV*), forming a kind of valve.

The mesenteron is a tube of fairly uniform calibre extending from the hinder part of the second thoracic segment to the region of the seventh or eighth abdominal segment and varies from eight to ten millimetres in length. Stained surface preparations of the mesenteron show externally a series of longitudinal muscle bands beneath which may be seen a layer of circular muscle fibres. Fig. 6 represents a transverse section of the mesenteron in its posterior region. Internally the epithelial cells are seen in both the secretory phase (*AE*) and the quiescent phase (*IE*). When actively secreting the cells elongate in a radial direction and vesicles containing fluid are "nipped off" and mingle with the alimentary matter lying on the lumen of the gut. The presumptive evidence is very strong that those vesicles contain the digestive ferments. Numbers of these vesicles could be observed lying in the lumen of the mesenteron (Fig. 6, *VS*) and the digestive ferments probably pass out by a process of dialysis and mix with the food material. There is no peritrophic membrane of any type in the gut of the wireworm (*Agriotes obscurus*).

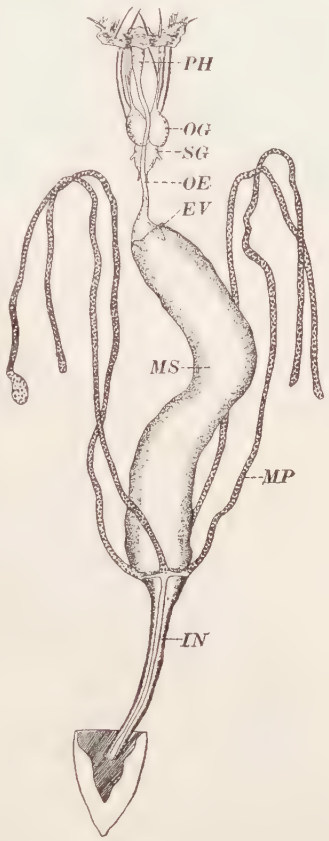

Fig. 4. The alimentary canal of *Agriotes obscurus* (larva) with part of the central nervous system. ×50. *EV*, oesophageal valve; *IN*, small intestine; *MP*, malpighian tube; *MS*, mesenteron; *OE*, oesophagus; *OG*, supra oesophageal ganglion; *PH*, pharynx; *SG*, sub-oesophageal ganglion.

The epithelial lining is thicker and usually more active in the middle region of the mesenteron and there is a greater tendency for it to be thrown into folds. There does not appear to be any differentiation of the epithelium into absorbent and secretory cells although the less active epithelial cells near the posterior end of the mesenteron may have a specialised absorbing function. The outer ends of the epithelial cells rest on a basement membrane (Fig. 6, *BM*). Groups of small cells with darkly staining nuclei (Fig. 6, *CC*) are to be seen at intervals beneath the epithelium.

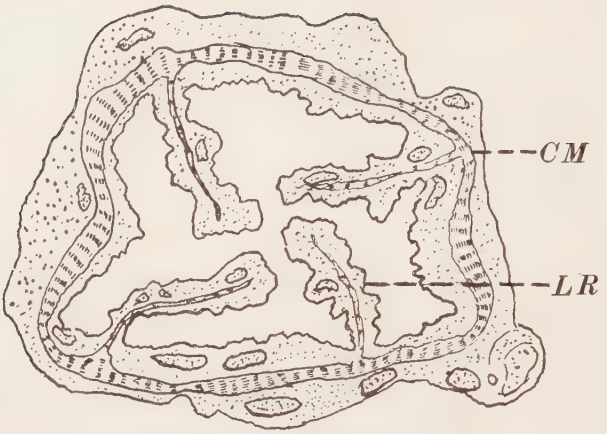

Fig. 5. A transverse section of the oesophagus showing the four longitudinal ridges which project into the lumen of the tube throughout its length. ×600 diams. *CM*, circular muscular layer; *LR*, longitudinal ridge.

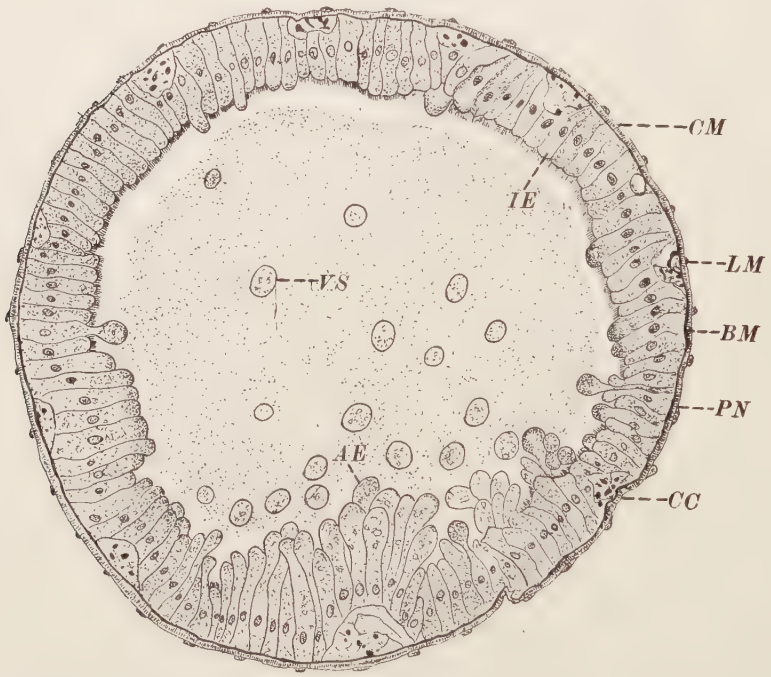

Fig. 6. A transverse section of the mesenteron near its posterior extremity showing the epithelial cells in both secretory and resting phases. ×300 diams. Drawn from sections 6μ in thickness. *AE*, epithelial cells in active secretory phase; *BM*, basement membrane; *CC*, crypt cells; *CM*, Circular muscle layer; *IE*, epithelial cells in the resting phase; *LM*, longitudinal muscle layer; *PN*, peritoneal layer; *VS*, a vesicle from a secretory epithelial cell.

Similar groups of cells were described by Gehuchten(4) in *Ptychoptera contaminata* and this writer named them crypt cells because they occurred in the hollows beneath the folds of epithelium. Gehuchten regarded them as centres of regeneration for epithelial cells.

Covering the outer surface of the mesenteron is a thin sheet of connective tissue which corresponds to the peritoneal layer of some other insects (Fig. 6, *PN*). The contents of the mesenteron when dissected out in double distilled water immediately after killing gave an alkaline reaction to Bromothymol blue and the *p*H lay between seven and eight.

The walls of the mesenteron gave a similar reaction. The hindgut

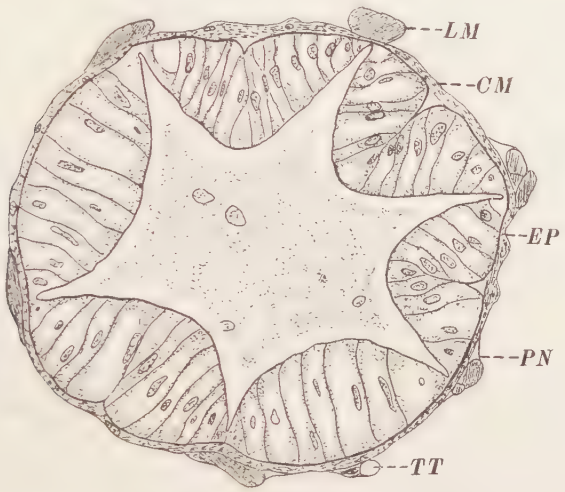

Fig. 7. A transverse section of the hindgut in the region of its middle third. ×500 diams. *CM*, circular muscle layer; *EP*, epithelium; *LM*, longitudinal muscle band; *PN*, peritoneal layer; *TT*, tracheal tube.

measures from 3 to 5 mm. in length and there is no differentiation into intestinal and rectal regions (Fig. 4, *IN*). The walls are composed internally of a layer of large epithelial cells which are grouped into six ridges for the greater part of its length (Fig. 7, *EP*). There is, however, a region midway along the hindgut where two pairs of ridges gradually run together, thus reducing the number to four, two large ridges alternating with two small ones. Posteriorly again the two large ridges split to re-form the original six ridges but these become very irregular in shape and size near the anal region.

The nuclei of the epithelial cells vary in shape but are usually somewhat elongated with the long axis radially directed.

The epithelium rests on a basement membrane and external to the latter is a layer of striated circular muscle fibres. Six comparatively large muscle bands lie outside the circular muscles and each of these bands alternates with an internal ridge of epithelium. Enveloping all these structures is a thin lining of connective tissue (Fig. 7, *PN*). The chitinous intima which lines this region of the gut is thicker in the anal region. Anal and rectal glands are absent. The alimentary canal opens to the exterior through a longitudinal slit on an anal papilla (Fig. 1, *AN*) situated on the anterior ventral surface of the last abdominal segment.

5. The Malpighian Tubes.

The malpighian tubes in both *Agriotes obscurus* and *Athous haemorrhoidalis* consist of four rather long yellow tubes whose distal extremities terminate freely (Fig. 4, *MP*), there being no secondary attachment to the gut or to each other such as occurs in the larvae of certain other Coleoptera. Occasionally the tubes are coloured very dark brown to black in irregular patches which vary in length from 1 to 3 mm.

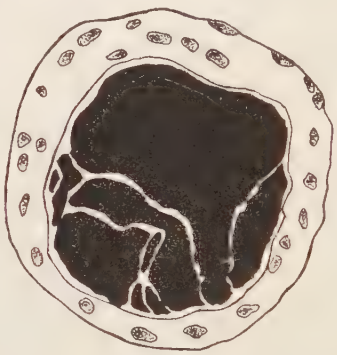

Fig. 8. A transverse section of a malpighian tube showing the lumen occluded with black excretory matter. Drawn from sections 15 μ thick. $\times 800$ diams.

An examination of sections of the darkened parts of the tube revealed that their lumina were completely occluded with a mass of non-crystalline excretory matter which gave the characteristic colour to that part of the tube (Fig. 8).

The malpighian tubes when dissected out in double distilled water and immediately transferred to indicators gave a decided acid reaction in bromothymol blue but was alkaline in bromophenol blue. The latter indicator has a range of *p*H 2·8–4·6. The hindgut reacted in a similar manner to these indicators. The cells lining the lumen of the malphighian tubes near their proximal ends are smaller and more regular in shape than those nearer the distal extremities and a considerably greater number of the former are required to line the periphery of the tube. The muscular layer of the hindgut sends some of its fibres along the malpighian tubes and the latter may be capable of some independent motion, but this was not observed.

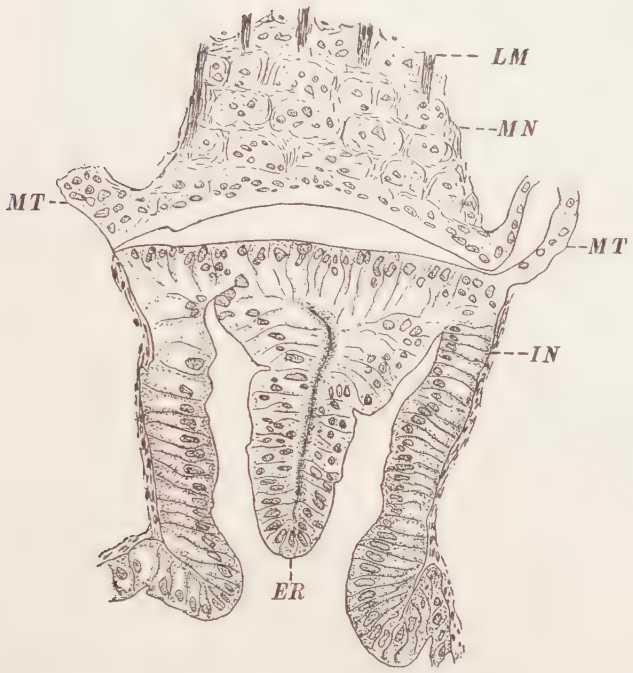

Fig. 9. An oblique section through the alimentary canal at the junction of the mesenteron and the hindgut showing the opening of one of the malpighian tubes into the gut. Drawn from sections 6 μ thick. $\times$300 diams. *ER*, an epithelial ridge of the small intestine; *MN*, mesenteron; *MT*, malpighian tube; *LM*, longitudinal muscle of mesenteron; *IN*, small intestine.

6. The Central Nervous System, Dorsal Vessel and Fat Body.

The central nervous system consists of the usual pair of supra-oesophageal ganglia (Fig. 4, *OG*) which lie above the oesophagus in the prothorax and send forward numerous nerves into the cephalic region.

The sub-oesophageal ganglia (Fig. 4, *SG*) whose double natures are not obvious lie close up to the supra-oesophageal ganglia.

The connectives which join the three thoracic ganglion masses together are double but those connecting the eight abdominal masses appear as single cords. The connective joining the last two abdominal nerve centres is very short and there appears to be a tendency towards coalescence. The dorsal vessel was also observed and consists of a non-septate tube extending nearly the whole length of the animal.

The fat body consists of narrow leaf-like folds sometimes of extraordinary length which may entirely disappear in larvae which have been starved for some considerable time.

Summary.

The structural evidence obtained from the study of the pits on the ninth abdominal segment of *Agriotes obscurus* favours the view that they are a pair of muscular impressions. The hairs lining the pit walls do not possess a nervous supply nor was any special nervous supply traceable to the pits as a whole. No structures which have been associated with sense reception in insects were found in the neighbourhood of the pits. There was no evidence that the pits are a modified pair of spiracles as was suggested by one writer (6).

With regard to the alimentary canal there are no salivary glands. The oesophagus possesses four ridges which project into its lumen and their muscular nature suggests that they are capable of independent movement.

The mesenteron is devoid of gastric coeca and does not contain a peritrophic membrane of any type.

The digestive fluid is secreted in vesicles which are budded off from the epithelial cells lining the midgut. The contents of the mesenteron has a *p*H of between seven and eight which is similar to the reaction of its cell walls. The hindgut is a straight tube without clearly marked intestinal and rectal regions and there are no glands of any kind in this part of the gut.

The malpighian tubes are four in number and are generally of a yellow colour, but it is not unusual to find blackened patches in the tubes which are due to dark masses of excretory matter blocking the tube.

The dorsal vessel is non-septate.

Besides the supra- and sub-oesophageal ganglia there are 11 nerve masses in the central nerve chain—three thoracic and eight abdominal.

The masses of fat body are characterised by their leaf-like shape and great length.

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(*Received* 1*st February*, 1927.)

THE BIOLOGY OF THYSANOPTERA WITH REFERENCE TO THE COTTON PLANT

1. THE RELATION BETWEEN DEGREE OF INFESTATION AND WATER SUPPLIED

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(With 3 Text-figures.)

An opinion prevails among many entomologists who have studied outbreaks of Thysanoptera in various parts of the world, that epidemic damage from certain species is connected in some way with abnormal meteorological conditions, and in particular with sub-normal rainfall.

It must be emphasised that this opinion rests more upon observation than upon precise experiment, and so expresses rather the point of view of the particular observer than any concrete phenomenon. The views of different observers concerning the same insect are thus sometimes contradictory.

With regard to *Heliothrips rubrocinctus* Giard., the Cacao Thrips, a serious pest of cacao, mango, avocado and other plants in the West Indies, Surinam, Brazil, San Thomé, Gold Coast Colony, Florida and elsewhere; decrease during the rainy season seems due to conditions unfavourable to multiplication; the greatest abundance is in times of drought (Reyne, A., 1921, Surinam). Weather conditions seem to have a very considerable influence upon the abundance of thrips; if, during the normal dry season there are frequent showers, thrips are likely to be more numerous; the reason for this is not definitely known (Ballou, H. A., 1919, Grenada). New shoots on cacao appear at the beginning of the rainy season, and it is then that thrips begin to multiply on the cacao trees, the maximum appearance being just after the heavy rains of May and June; a certain degree of moisture seems to be necessary for the development of the thrips; at the height of the dry season they are at their lowest ebb, although the damage done by them may be most apparent at that time; thrips are naturally controlled by heavy showers of rain and by excessive drought (Urich, F. W., 1916, Grenada).

On one estate, two periods of abundance of thrips occurred during the year, one in April and May, in the dry season, and the other in September and October, in the wet season. (*Agric. News*, Barbadoes, 1916, *re* St Vincent.) *Heliothrips rubrocinctus* seriously attacked and defoliated cacao especially in dry localities or during dry weather (Ritchie, A. H., 1916, Jamaica).

With regard to *Thrips tabaci* Lind, the Onion Thrips, a cosmopolitan pest of many cultivated plants, the periodicity of epidemics is in direct relation to the temperature and rainfall during June, July and August; a temperature above normal, and rainfall below normal, are factors that favour development and are unfavourable to the proper growth of the onion plant (Horsfall, J. L. and Fenton, F. A., 1922, Iowa). As a rule, when onions are planted, the dry season is not completely established and the first onion crop, lasting about two months, suffers little from thrips if sufficient water be present; there may be a second good crop, unless water be scarce, in which case, as in that of a third crop, a considerable loss occurs owing to infestation (Van Heurn, W. C., 1923, Java).

With regard to *Euthrips nicotianae* Hinds., the Tobacco Thrips, it is quite evident that the amount of injury by thrips will vary from year to year, depending upon the period and amount of rainfall (Hooker, W. A., 1907, Florida and Georgia).

With regard to *Scirtothrips citri* Moul, the Citrus Thrips of California, the number of generations is greater in exceptionally long, hot summers than in more moderate ones. Cool, cloudy or rainy weather markedly diminishes the various activities of the insects (Horton, 1918, California).

With regard to *Heliothrips indicus* Bagn., the Cotton Thrips, during the rainy season the thrips is difficult to find and only becomes effective after the rains have more or less ceased (Bedford, H. W., 1921, Sudan).

Many more quotations concerning this question could be given, but these will suffice.

Application of the belief that thrip epidemics are correlated with unusually dry conditions, to the practical control of an epidemic, has only been suggested, to the author's knowledge, by Hooker, who indicated in 1907 the noticeable effect of sprinkler irrigation in decreasing the numbers of *Euthrips nicotianae* upon tobacco plants, and the inability of surface irrigation to produce such a decrease; and by Corbett (1919) and Bedford (1921), who have recommended, against *Heliothrips indicus* in the Gezira cotton growing area of the Sudan, an increase in

the water supply of furrow irrigated cotton from 450 cm. per feddan (= 1·038 acres) to 550 or even 600 cm., every 15 days.

Scope of the present experiments.

The series of experiments which are described in this paper were devised in order to decide:

(*a*) whether the degree, to which a species of Thysanoptera may infest a species of plant, can vary with the amount of water the plant receives;

(*b*) whether, if such correlation be established, there is any difference between rainfall and irrigation in this respect;

(*c*) whether there is any correlation between the degree of infestation and the interval of time which elapses between successive waterings of the plant.

The experiments were carried out under glasshouse conditions in Manchester during, as regards preliminary experiments, the summers of 1924 and 1925, and as regards the main experiments, the summer and autumn of 1926. About 300 cotton plants were used each year, chiefly of the Egyptian Sakellarides variety, and long staple American Upland varieties.

The species of thrips used in the experiments was *Thrips tabaci* Lind., which is in very many respects one of the most suitable species for such experiments. The biology and life-cycle of this insect will be discussed in later papers. It is sufficient here to indicate that this species possesses the following suitable qualifications.

(1) It is cosmopolitan, a severe pest of many plants in such climatically different areas as South Europe, West and Central Europe, Asiatic Russia, India, Java, Australia, Hawaii, Chili, Mexico, the United States, and Canada.

(2) Although not itself a recorded pest of cotton, it attacks cotton plants with avidity, producing lesions almost indistinguishable from those produced by *Heliothrips indicus*, the cotton thrips of the Sudan, and by *Thrips flavus*, the cotton thrips of Turkestan. It is the most closely related species to the latter form.

(3) It is particularly a species which appears in the form of sporadic and severe epidemics; such outbreaks have been recorded in areas so separated geographically as Iowa, France, Java and Queensland, and have been correlated by observers with drought conditions.

Objections to glasshouse experiments.

There are of course certain serious objections that can be raised against experiments of this nature carried out under glasshouse conditions. In the first place, it might appear that the blocks of plants are too small numerically to permit of definite conclusions being drawn from the data thus obtained, and, in the second place, that the degree of insect infestation is higher than occurs normally in the field, since the plants are living under abnormal conditions of water supply, atmospheric humidity, crowding, root freedom, and so forth, whilst the insects concerned are protected from enemies and from adverse climatic conditions. Whilst admitting that glasshouse experiments are valuable only as a guide to the lines upon which large scale field experiments can profitably be conducted, and that field tests must be the final arbiters of the conclusions drawn from such glasshouse experiments, it must be emphasised that they permit of more precise control of temperature and water supply, and of a much more accurate conception of the degree of insect infestation, than can be obtained under field conditions. The plants, themselves, though from the same strain of seed, were finer and healthier plants vegetatively than were those in the Egyptian or Sudanese fields, owing possibly to the calmer and more humid atmosphere, and the lower sun temperatures, of the glasshouse; and although they were inferior in production of flowers and bolls, would be little inferior in the number of ripe bolls produced, were the glasshouses situated in a sunnier situation than the confines of an industrial city, since the degree of boll shedding was lower than in their native area.

As regards the degree of insect infection, it was probably higher under glasshouse conditions than in the case of ordinary endemic attack in the field, but probably much below the severity of infestation during an epidemic.

Conditions of temperature and humidity.

With regard to the mean values for temperature and atmospheric humidity in a glasshouse, it is evident that whereas temperature is, within limits, controllable, the humidity is not thus controllable, and when considerably heavy amounts of water are being applied to plants, the mean relative humidity will approach saturation.

It was necessary therefore to carry out a series of experiments with the object of establishing:

(*a*) the optimum temperature for the development of the life-cycle stages of *Thrips tabaci* in a saturated atmosphere;

(*b*) the water supply required by cotton plants grown at this particular temperature and at a high degree of relative humidity.

The experiments concerning the optimum temperature for the insect will be described in a later paper. It may be stated briefly that the value arrived at was 20–22° C.

The value of water supply arrived at, for Egyptian and American plants grown in pots of 22–23 cm. diameter at the soil surface, in a mean temperature of 20–22° C. and at degrees of humidity between 80 and 100, was 300 c.c. of water per pot at intervals of three days. This is equivalent to 75 mm. of rainfall, or approximately 300 cm. of irrigation water per acre, per month. Throughout the experimental work of 1926, therefore, the temperature of the glasshouse was controlled, as far as possible, so as to give a mean value of 21° C. Actually, owing to fuel shortage, the mean temperature attained was 19° C., the mean maximum being 26·7° C. and the mean minimum being 11·25° C.

The mean maximum and minimum relative humidities throughout the period were 92·4 per cent. and 74·7 per cent. respectively.

The estimation of intensity of infestation.

In order to be in a position to compare the intensity of thrip infestation of different blocks of plants throughout the period, a sufficiently accurate method of measuring the degree of infestation had to be devised.

There is no standardised method of estimating the density of insect attack that can be satisfactorily applied to foliage insects in general. Three lines of approaching the problem were possible:

1. Estimation of the *physiological* effect of insect attack upon the plant, by comparison of the amount of leaf shedding, flower production, square shedding and boll shedding of infested plants and uninfested plants.

2. Estimation of the *morphological* effect of insect attack upon the plant by obtaining the ratio of damaged to undamaged leaves.

3. Estimation of the *actual numbers* of insects upon the plant by counting.

The first method was impracticable, since many factors beside insect attack can influence leaf shedding or boll shedding or flower production.

The second method was also unsatisfactory since extensive leaf damage is no indication of correspondingly severe thrip infestation. Severely damaged leaves are generally free from thrips. Further a lightly attacked leaf may in time develop intensely rusty, necrosed areas.

The third method is impracticable, if precise accuracy be required, since, ideally, every stage of the insect on each plant of each block would have to be counted, and the minute size of these stages, together with the large number of them that may occur on a plant, would render the method inexpressibly tedious and slow. Even if only a certain number of leaves be examined, as was done by Reyne, there is the disadvantage that since leaves vary in size, such a count is useless for comparison with other blocks or with blocks of another species of plant.

The method actually adopted was to take, at intervals throughout the summer, a number of leaves from each block of plants, to measure the area of each leaf with a planimeter, to count the number of adult and larval thrips on each leaf, and to obtain for the sample of leaves a definite numerical *infestation factor* which expressed the number of adults or larvae per 100 sq. cm. of leaf surface. This factor was considered to represent the intensity of infection of that particular block of plants at that particular time.

The leaves were selected at random, but very young leaves and severely damaged leaves were avoided, since they were almost invariably free from thrips. Estimation of the intensity of infestation of each block was commenced only after the block had been subjected to a definite water supply for at least four weeks.

The method is of course not precise. Errors occur in measuring the area of each leaf. Errors in counting the number of thrips per leaf, since, when several hundred stages are present, even though the count be made with the help of a binocular microscope, small and partly concealed individuals are liable to become overlooked. The method however is sufficiently accurate to indicate differences in the degree of infestation of different blocks of plants, and although each leaf requires an examination lasting three to five minutes, the operation is incomparably quicker and less tedious than would be an attempt to count the insects on leaves still on the plant.

The method has the advantage of permitting comparison between blocks of plants of different ages and sizes, between plants of different varieties, and between plants of different species.

The value of the data thus obtained is dependent upon:

(*a*) the number of plants examined;

(*b*) the frequency of examination;

(*c*) the purity of infection;

(*d*) the non-migration of thrip stages between adjacent blocks.

Not more than one or two leaves per plant can be removed at each examination if the plant is not to be affected by defoliation. Actually only 10–20 leaves per block were taken at each examination, although each block contained 30–50 plants. Each block was examined at least four times within a month, that is to say within the average length of the thrip life-cycle.

The purity of infection throughout the experiments was very high. Occasional specimens of *Parthenothrips dracaenae* that occurred in early summer were easily noted and avoided when counting. No other species of Thysanoptera were present. There was no other cotton attacking pest such as Greenhouse Whitefly or Red Spider, beyond a slight infection of a few plants of one block by the aphid *Myzus persicae* during August 1926, and a slight attack by an unidentified Tortricid caterpillar during the same period.

The migratory powers of *Thrips tabaci* depend very largely upon the agency of wind. In an absolutely calm atmosphere, the insect can only leap from one leaf to another in close proximity, or, in the case of small plants, can travel from one plant to another by leaping along the ground. In a glasshouse, air currents are present to a slight extent, and a certain amount of migration of adult thrips occurs between blocks. It must be noted however that the thrips, after emerging from the pupal stage, climbs the nearest plant, works its way upward from leaf to leaf until it has found a lower leaf surface sufficiently clear to its liking, whereupon it commences to feed and to oviposit. Such oviposition is invariably upon the lower surface, and the insect probably only travels to the upper leaf surface after oviposition is over. That is to say, migrating thrips have in most cases already oviposited on the plant near whose base they emerged. In any case, there is no migration of larval stages from block to block.

Under glasshouse conditions therefore, the infestation of a series of adjacent blocks of plants can be compared throughout a season with a fair degree of accuracy, since the infection of each block is uniform, and a block is not reinforced greatly in number of adult thrips from an adjacent block, and in larval thrips not at all, providing that a sufficient interval between blocks be maintained.

In the field such comparison is difficult owing to the close proximity of plants and to the occurrence of wind. Even in one block, under field conditions, the windward edge may be heavily infested and the leeward edge relatively free.

In calculating the infestation factor, it is advisable to examine both

surfaces of the leaf and to double the value of each measured leaf surface since, although in the great majority of cases, the insects occur only on the lower surface, examples occur of both surfaces being infested by adults or larvae, owing to overcrowding or to severe surface damage of the lower foliage surface.

The highest value obtained for the infestation factor was, in the case of adults 27, and in the case of larvae 111 individuals per 100 sq. cm. of leaf surface. Both values occurred on a particular block of American cotton during late July and early August. The largest number of adults on an individual leaf was 84, and of larvae 392, again on American cotton. Counts of round about 200 larvae per leaf were common.

Four series of experiments were carried out.

Series I.

Three blocks of plants, *E*, *F*, and *G* were taken. Blocks *F* and *G* were plants grown from severely selected Sakellarides seed of the 1924 Egyptian crop. Block *E* was from seed of the Maarad variety, an Egyptian mutant from the Arizona strain of Pima cotton, itself a descendant of the Egyptian variety Abbassi, and very similar to Sakellarides. The plants in each block were 20 cm. apart, the blocks were 60 cm. apart. The plants were grown in pots of 23 cm. diameter at the soil surface, whose drainage holes had been plugged with cement. The soil was a medium clay loam.

These blocks were watered at intervals of five days. *E* received the equivalent of 150 mm. of rainfall, or approximately 600 cm. of water per acre, per month; *F* received half this amount; *G* received one-fifth of this amount. The water was applied to the soil surface, care being taken to avoid splashing the foliage. Block *E* thus received an excessive water supply; block *F* a sufficient water supply; block *G* a deficient water supply. This was reflected in the appearance of the plants, block *E* comprising tall plants with numerous large succulent leaves, block *F* having plants similar in appearance to those in the field, and block *G* being composed of stunted plants with scanty, leathery, small leaves, the plants resembling the volunteer plants which may occur on fallow, unirrigated areas of the cotton field.

Fig. 1 indicates the degree of infestation of both adult and larval thrips on these blocks throughout the months of August and September, when infestation was highest. As shown by these curves, the infestation factor varied inversely with the amount of water supplied throughout the period; the mean infestation factor for the adults was, for *E*, *F* and

G, 0·42, 2·26 and 6·26 respectively; for larvae it was 2·85, 6·37 and 10·8 respectively.

If however the actual number of thrip stages per leaf be considered, it may be noted that *E* had 0·6 adults and 3·5 larvae, *F* had 2·3 adults and 6·9 larvae, *G* had 2·3 adults and 5·8 larvae per leaf. That is to say, these experiments suggest that excessive water supply may be accom-

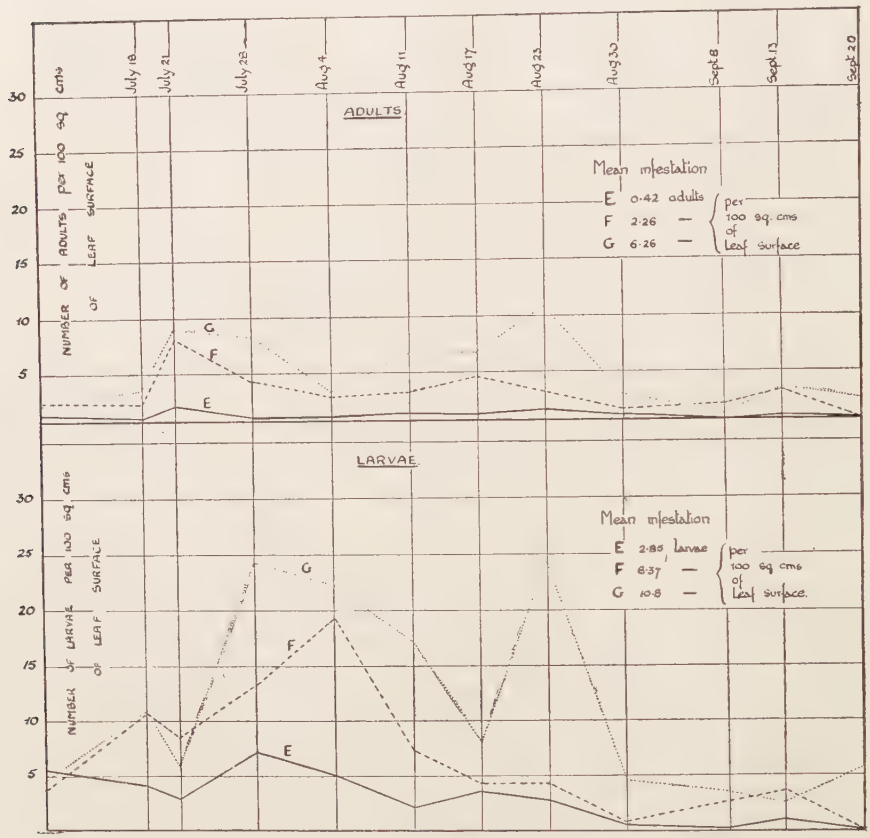

Fig. 1. The degree of infestation of three blocks of Egyptian cotton. *E*, *F*, *G*, receiving differing water supplies.

panied by a low infestation factor and by an actual low number of stages per leaf, as compared with plants receiving normal water supply.

Among plants suffering from water deficiency, the actual number of thrip stages per leaf may be lower than in the case of plants receiving normal watering, but owing to the smaller foliage surface the infestation factor will be greater and the plants will suffer more severely.

Series II.

Two blocks of cotton, *X* and *Za*, were taken, each comprising about 50 plants of a strain of Webber cotton, an American Upland long staple variety, from seed of the 1925 crop of the Zeidab estate of the Sudan Plantations Syndicate. The size and arrangement of pots was as before. Block *Za* was watered by a revolving sprinkler in a portion of the house that could be shut off from the rest by waterproof curtains. The height, speed and nozzle apertures of the sprinkler were so adjusted as to imitate fairly closely a heavy shower, and such a shower was applied at intervals varying from two to five days, the amount of rainfall at each application varying between 10 and 30 mm. but being always precisely recorded in a gauge. The rainfall intensity thus obtained was approximately 50 mm. per hour. The monthly rainfall simulated was that normally recorded in the Mongalla district of the southern Sudan, a district where long staple Upland cotton is being experimented with as a rain crop (Wardle, 1926).

Block *X*, on the other hand, was subjected to an irrigation system of watering, each plant receiving an amount of water equivalent in depth of millimetres to that which each of the *Za* plants was receiving, the watering of both blocks being carried out at the one time; that is to say, at the same time that the *Za* plants were receiving a sprinkler fall of, for example, 15 mm., the *X* plants were each receiving the equivalent of 15 mm. applied carefully to the soil surface of each pot.

The actual quantities of water applied each month were as follows:

	May	*June*	*July*	*August*	*September*
Za	130	110	120	160	90 mm.
X	5395	4565	4980	6640	3735 c.cm. per pot.

Thus the monthly totals were in each case in excess of normal requirements under glasshouse conditions.

Fig. 2 indicates the infestation factors throughout June, July, August and September. The curves show a marked difference between *X* and *Za* as regards the degree of infestation of both adults and larval thrips.

The mean infestation factors for block *X* for the whole period, were, for adults and larvae 6·58 and 16·8 respectively; for *Za*, the factors were 9·16 and 27·5 respectively.

The mean number of adults and larvae per leaf were, for block *X*, 7·2 and 17·1 respectively, and for block *Za*, 9·16 and 27·5 respectively. The close agreement of the actual numbers per leaf with the numbers

per 100 sq. cm. of leaf surface is due to the fact that if a large number of leaves of American plants be measured the total surface area of both sides of a leaf will be found to approximate to 100 sq. cm.

That is to say, the plants subject to irrigation were less infected on the whole than were those subject to rainfall, despite the fact that the

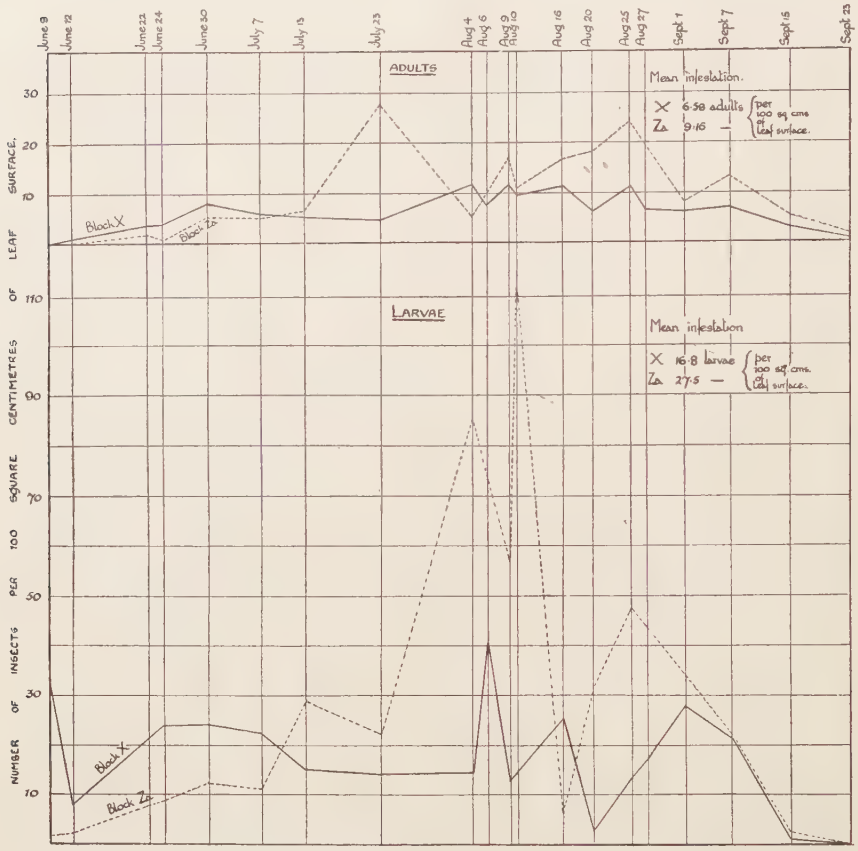

Fig. 2. The degrees of infestation of irrigated and of rainfall. American cotton with identical monthly water supplies.

amount of water supplied and the watering dates were identical. It may be noted however that up to July 10, block *X* was more infected than block *Za*, but after this date, as the plants became leafier and as, presumably, less water actually reached the soil level of *Za* than of *X*, the position became reversed.

These results oppose the view that the minimising effect of heavy

water supply is brought about solely by mechanical removal of thrip stages from the foliage. In the case of *Thrips tabaci*, both adults and larvae are negatively phototropic, quickly migrating under experimental conditions from a sun-illuminated side of a leaf to the shady side. On the plant, however, when the under surface of a leaf is excessively crowded, the hunger stimulus brings them to the upper surface, even when fully exposed to the sun; they are however very restless under such conditions. This migration to the upper surface is more marked when the leaf is shaded by others or when the sky is overcast. Adult thrips on the upper surface of a leaf are readily removed by spraying or by shaking the leaf, but larvae cling more tenaciously to the leaf.

The infestation factors for adults and larvae were obtained just before watering, and just after watering with the sprinkler on several occasions, and the results obtained suggest that the number of adults may be reduced considerably by the mechanical action of falling water, but that the reduction of larval numbers is slight. It is very possible however that many adults knocked from the plant succeed in getting back on to the plant again.

It is possible however that in a rainfall climate, a species of Thysanoptera, which lives habitually on the upper foliage surface, may be affected numerically by intense heavy periods of rain, or in a dry climate may be so affected by heavy and careless irrigation, but that some additional explanation for the influence of heavy water supply upon thrip infestation is necessary seems indicated by the greater influence of irrigation watering over sprinkler watering in the experiments.

Series III.

This series comprised experiments devised to test the effect of water contact upon thrips stages. Batches of first-stage and second-stage larvae, of prepupae and pupae and of adults, were floated on the surface of water in closed vessels, and batches were placed in waterlogged soil in closed vessels.

Despite the fact that the insects were thus deprived of food, and were subjected to more prolonged and more intense contact with water than could occur under normal field conditions, the stages were very resistant.

No adults died within six hours, about 20 per cent. within 12 hours, 50 to 75 per cent. within 24 hours. All were dead within two days.

Of second stage larvae, 30 per cent. died within 24 hours, about 50 per cent. within two days, the rest within three days. First stage larvae

were less resistant, but the absence of food may have affected them. Prepupae and pupae were very resistant, very few dying within two days and many eventually becoming adults after several days' water contact. In a series of experiments conducted by my colleague Miss E. I. MacGill, second stage larval thrips were reared in glass chambers in which the relative humidity could be kept constant by the use of mixtures of sulphuric acid and water. The laboratory temperature fluctuated between 10·5 and 20·5° C.

At 100 degrees of relative humidity, 8·5 per cent. of larvae were reared through to the adult condition. At 20 degrees of humidity, 2·2 per cent. of larvae were reared through.

When prepupal stages were used at 100 per cent. of relative humidity, 40 per cent. of prepupae were reared to the adult condition; at 20 per cent., 37·5 per cent. were reared through; at absolute dryness 16·6 per cent. were reared through. Thus, although a large percentage of larvae and prepupae died before reaching the imaginal condition, such mortality seems due to the unnatural rearing conditions rather than to the influence of a high degree of humidity.

The results of this series of experiments therefore show that while certain stages of thrips can be killed by prolonged contact with water, they are not affected adversely by a saturated atmosphere.

Series IV.

Four blocks of plants were taken, *A*, *B*, *C* and *D* respectively, all comprising plants from Sakellarides seed of the Egyptian 1924 crop. These blocks were grown in the ground in a stiff clay loam. In blocks *A* and *B* the plants were grown on ridges; in *C* and *D* they were grown on the flat soil surface.

These blocks received water applied to the ground surface precisely as under irrigation conditions; each block received the equivalent of 225 mm. of rainfall, or approximately 900 c.m. of water per acre, per month. The monthly total was applied in equal instalments at intervals varying for each block; thus *A* received the equivalent of 90 mm. every 12 days, *B* the equivalent of 60 mm. every 8 days, *C* the equivalent of 30 mm. every 4 days, and *D* the equivalent of 15 mm. every 2 days. A water supply of 900 c.m. per acre per month would not be excessive under the conditions of low humidity, high sun temperature, and high rate of surface evaporation in such an area as Arizona, Mesopotamia or the Sudan, but under glasshouse conditions it is grossly excessive, being in this case three times what is necessary. In the case of block *D* the

soil was perpetually under water. All the plants grew excessively tall and strong, and had huge leaves and few flowers.

The degree of thrip infestation throughout the period was low. The curves of the infestation factors are given in Fig. 3.

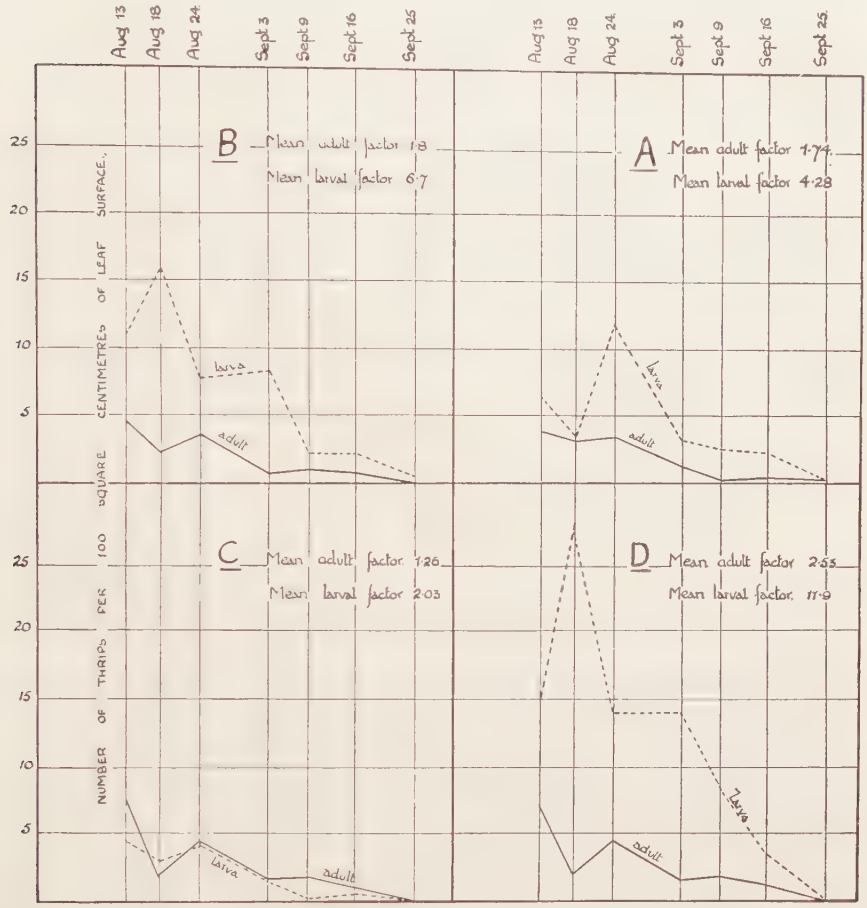

Fig. 3. The degrees of infestation of four blocks of Egyptian cotton receiving identical monthly water supply but at differing intervals.

It will be noted that block *C* was the least infested, *A* the next, then *B* and then *D*, the respective mean factors being, as regards adult infestation, 1·26, 1·74, 1·8 and 2·53; and as regards larval infestation, 2·03, 4·28, 6·7 and 11·9 respectively. The close similarity between the mean factors for adult infestation is probably due to the fact that,

owing to the excessive vegetative growth of these blocks, the branches of one block tended to overlap those of adjacent blocks and so to offer a path of migration for adult thrips from one block to another. An attempt to isolate the blocks by intervening hedges of *Cajanus indicus* was unsuccessful, as these plants, although in the Sudan apparently avoided by *Heliothrips indicus*, were attacked as freely as were cotton plants and thus merely aided migration of the adult thrips from one block to another. Such adult migration however seems to occur after oviposition, and there is no larval migration between adjacent blocks, so that the curves of larval infestations give a more correct conception of the discrepancy between the mean infestations of the different blocks. The results of this series of experiments suggest that mere weight of water is not the only factor in bringing about a reduction in the degree of thrip infestation, but that the nature of the ground surface or the intervals between watering probably play a part.

Block *C* had a flat ground surface, water was applied every four days, and the soil surface although moist was firm and caked between waterings; block *A* had a ridged surface, but owing to the amount of water applied at each watering these ridges were completely covered, and for a few days after watering were compact, but, before the next watering date, had become loose and powdery; block *B* had also a ridged surface, but the water was never deep enough at each watering to cover the crests of the ridges, which were therefore always somewhat loose; block *D* had a flat surface but was almost always under a few millimetres of water.

It may be added that since all the plants received the same quantity of water per month, all were about the same height and same stage of development. There is no reason to believe that the blocks differed from one another, as regards concentration of cell sap, thickness of cuticle, or other morphological features, so markedly as did the degrees of larval infestation upon them. As regards age, only 20 days separated the earliest sown block from the latest.

General conclusions.

It is probable that in very many cases the effect of heavy rainfall or of heavy irrigation in reducing thrip infestation is more apparent than real. Increase of water supply stimulates the growth of individual leaves and the production of new leaves, so that the numerical ratio of thrip stages to unit area of foliage surface is lowered, and the ratio of damaged to undamaged leaves is lowered. The plants will therefore

appear to suffer less from thrip damage, and may actually do so although no numerical decrease of thrips may have been brought about. Further, under field conditions, where the chief danger to the plant from thrip attack arises from the defoliation caused by premature and undue leaf shedding, any meteorological phenomena or soil conditions which increase such leaf shedding or which reduce it, will magnify or will minimise, as the case may be, the damage resulting from thrip attack. That is to say, it is conceivable that of two adjacent districts, each with identical degrees of thrip infestation, but differing from one another as regards soil conditions and exposure to wind, the plants of one district may show severe injury, those of the other district may be scarcely affected. The results of these experiments however support the view that a correlation exists between the degree of infestation of *Thrips tabaci* upon cotton plants, and the amount of water the plants receive. They do not bear out the idea that the primary effect of watering is due to mechanical removal of thrip stages from foliage, or that the insects are readily killed by contact with water or waterlogged soil or inimically affected by a saturated atmosphere.

Further, there is no evidence that changes in the concentration of cell sap, induced in cotton plants of the same age by differing water duties, are sufficiently important to influence the degree of thrip infestation, although the migration of thrips from cotton in the field to such plants as lucerne (*Medicago sativa*) when the cotton is six or seven months old may be so influenced.

One reason for the influence of heavy rainfall or heavy irrigation watering upon the degree of infestation of certain thrip species probably lies in the phenomenon of surface caking to which certain types of soil are liable, when subjected to alternate periods of beating rain or heavy flooding, and of hot sunshine. In the case of those species of Thysanoptera whose larvae habitually descend into the surface layers of the soil to pupate, and whose emerging imagines must pass through the soil surface, such soil crusting, extending as it may do to a depth of several inches, may be a potent agent in limiting their numbers.

Towards the end of the summer of 1926, a number of pots containing Webber plants were selected at random, the plant in each cut down to within an inch from the surface. In the case of half the pots, the soil surface was kept dry and allowed to become loose and powdery; in the other pots, the surface was moistened and tamped down at intervals of a few days. From the dry powdery surface, 175 adult thrips emerged between September 9th and 20th. From the moistened crusted surfaces

only 49 thrips emerged during the same period. Further experiments were vitiated by the general disappearance of thrips from the cotton about this time, and more evidence is required, but the results obtained certainly suggest that the emergence of adults is influenced by the nature of the soil surface. The entrance of larvae into the soil to pupate is probably less affected by soil caking, since they can pupate away from soil. If the soil be completely under water, some larvae will pupate between fallen leaves or on the plant itself.

The effect of surface caking upon the thrip stages is probably one of suffocation brought about by the pressure of the clay particles.

The degree to which such surface caking occurs under the influence of rainfall or irrigation water, varies according to several factors. In soils with a low clay content, less than 15 per cent., such caking does not usually occur, the surface remaining loose and friable. With a clay content between 15 and 30 per cent., moderate showers tend to compact the soil, under temperate climatic conditions, and it will remain so compacted for a period of days. When the clay percentage is high, more violent water pressure is necessary, in the form of heavier rain showers or heavier irrigation waterings, and the duration of the crusted condition is shorter. Under conditions of high sun temperature, low humidity and consequently high surface evaporation, soils of high clay content do not remain compacted long but tend to dry rapidly, to shrink greatly, and to become fissured with large cracks.

The tendency of clay loams of humid, high rainfall areas to undergo surface caking may be of course reduced considerably by tillage, by the presence of calcium carbonate or calcium sulphate or humus in the soil, and by surface vegetation, so that, on the whole such areas afford favourable conditions for the endemic presence of soil pupating Thysanoptera and for epidemic attack during periods of long intervals between rainfall showers.

On the other hand, in arid or semi-arid areas, the tendency of the heavy clay, calcareous soils, to show surface pulverulence and so afford favourable thrip conditions, is offset by the almost invariable presence in such soils of sodium or potassium carbonate which, even in low percentage, favours soil compaction. Further, the native flora tends towards thickness of epidermis and so is antagonistic to thrip attack. That is to say, such areas are not favourable to the multiplication of Thysanoptera.

Scientific large scale cultivation of arid or semi-arid soils, such as occurs to-day in the Sudan, the south-west United States, Mesopotamia,

north-west India, and elsewhere, is a comparatively modern practice. Improved methods of tillage, of drainage, of deep furrow irrigation, of gypsum addition, and so forth, can neutralise the action of alkaline salts to some extent, and can enable the production of crops which under primitive conditions of agriculture would not tolerate such soils, such crops for example as long staple varieties of cotton, cruciferous crops, leguminous crops such as alfalfa (*Medicago sativa*), the latter plant a notoriously favourite food plant of thrip species in many parts of the world. That is to say, modern agricultural conditions tend to make semi-arid areas favourable for Thysanoptera, and if an adaptable species should become introduced into such an area, the tendency would be for it to become well established, to become endemic as regards damage, and severely so. The weight of water supply necessitated in such areas, owing to the high degree of surface evaporation, does of course tend to promote surface caking and so possibly to oppose thrip multiplication, but the value of this is offset by the long intervals between waterings, by tillage and by furrow irrigation in which the crests of the ridges are untouched by water and hence remain powdery. Such agricultural practices however are unavoidable in the case of the cotton plant, since the effect upon yield, induced by the lower degree and later appearance of flowering, and by lower boll production, which more frequent watering or tillage neglect would produce, would outweigh any possible advantages resultant from thrip production.

In conclusion, I must acknowledge my great indebtedness, for research facilities and for information, to the following: the Empire Cotton Growing Corporation, the Sudan Plantations Syndicate, Mr H. King, Mr H. W. Bedford and Mr Johnston of the Sudan Government Entomological Service, Mr Walley of the Gezira Research Farm, Mr C. B. Williams of the Egyptian Entomological Service, Mr Nichol of the Arizona Entomological Service, the staff of the Botanical Department of this University, Mr H. Britten of the Manchester Museum.

Summary.

1. Experiments concerning the degree of infestation of *Thrips tabaci* upon cotton plants under glasshouse conditions suggest that the *infestation factor*, or number of thrip stages per 100 sq. cm. of foliage surface, varies inversely with the weight of water supplied.

2. Plants receiving excessive water supply have a lower infestation factor and a lower number of thrip stages per leaf as compared with plants receiving sufficiency of water supply; plants receiving insufficient water supply have a greater infestation factor than plants receiving sufficiency of water supply but have not necessarily a greater number of thrip stages per leaf; owing to their smaller foliage area however they suffer more from thrip attack.

3. Irrigation is more effective in influencing the degree of thrip infestation than is rainfall.

4. Irrigation on a flat soil surface is more effective than irrigation on a furrowed soil surface.

5. The effect of excessive water supply does not appear to be due to mechanical removal of thrips stages from the foliage, nor an injurious effect of soil moisture or atmospheric moisture upon thrips stages, nor alteration of the osmotic concentration of cell sap, although all three factors may operate slightly.

6. It is suggested that one factor concerned is the influence of heavy water supply upon the texture of certain soils, in promoting surface caking which will act inimically to soil pupating species of Thysanoptera.

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(*Received 24th June,* 1927.)

THE BIOLOGY OF THYSANOPTERA WITH REFERENCE TO THE COTTON PLANT

2. THE RELATION BETWEEN TEMPERATURE AND LIFE CYCLE IN A SATURATED ATMOSPHERE

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(With 3 Text-figures.)

As indicated already in the first part of this paper, a correlation between the degree of infestation of a plant species by a thrip species, and the weight of water supply that the plant receives, is suggested by the results of experiments with *Thrips tabaci* Lind. infesting cotton plants under glasshouse conditions.

Under such conditions, the mean relative humidity throughout the experiments cannot be controlled so readily as can the mean temperature, and where water supply experiments are being carried out, the mean relative humidity may approach saturation. In this respect, of course, the environment of plant and insect will resemble that which prevails in the field immediately after heavy rainfall or heavy irrigation. It is therefore of some interest and importance to know the extent to which the metabolic processes of the insect are influenced by such high conditions of relative humidity, and particularly to establish the temperatures at which metabolism will be at its optimum, in so far as is indicated by the duration of life cycle stages, and by the percentage of transformations from one stage to the next.

The data put forward here is derived from experiments carried out under glasshouse conditions arranged, so far as possible, to simulate field conditions, and under laboratory conditions of constant temperatures and constant relative humidity percentages.

Of the laboratory data, however, only those obtained at a relative humidity of 100 per cent. will be discussed here.

The suitability of *Thrips tabaci* for these experiments has already been indicated. It may be stated briefly that this species is one of the most cosmopolitan species of Thysanoptera, having been recorded from Albania, Austria, Australia, Bermuda, Bessarabia, Bohemia, Dalmatia, England, Florida, France, Germany, Hawaii, Heligoland, Hungary, India, Italy, Java, North America, Russia, Sweden.

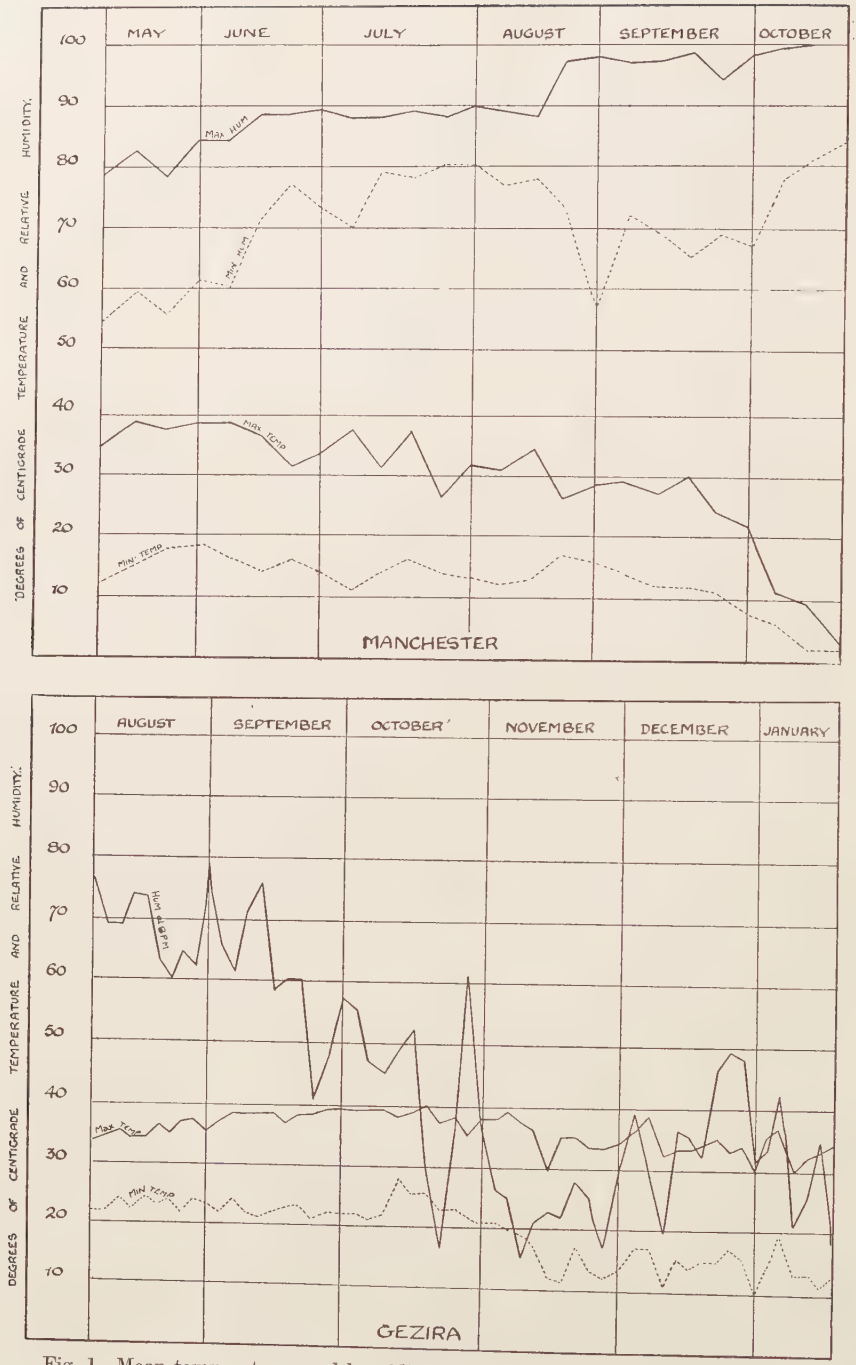

Fig. 1. Mean temperatures and humidities for Manchester (glasshouse) and the Sudan (Gezira).

That is to say, it is a species whose geographical range is not narrowly limited by climatic temperatures. It is further one of the most omnivorous of Thysanoptera, having been recorded from a very wide range of unrelated plants. It attacks cotton plants with avidity, producing lesions almost indistinguishable from those caused by the closely related *Thrips flavus* of Turkestan, and from those caused by *Heliothrips indicus* in the Sudan. Finally, it is particularly a species which occurs in the form of sporadic and severe epidemics.

In the glasshouse, the daily temperatures and relative humidities were recorded during the period May to October on a thermo-hydrograph. The mean weekly values are indicated in Fig. 1, and, for comparison, there are given the weekly mean temperatures and relative humidities for the Gezira district of the Sudan—an area where *Heliothrips indicus* is severely endemic upon cotton—for the period August to January, during which the thrips is active. As comparison between the respective curves will show, the chief difference between the two stations relates to humidity. Whereas the glasshouse humidity did not vary greatly around a mean of 84·5 per cent., the Gezira mean humidity fluctuates from a high value at the beginning of the season to a low value towards the end of the season.

On the other hand, the curve of Gezira temperatures is much more uniform than that of the glasshouse temperatures.

The appearance and disappearance of *Thrips tabaci* in the glasshouse are dependent upon temperature conditions. The appearance of *Heliothrips indicus* in cotton in the Sudan would seem, according to Bedford (1921) to be influenced by humidity conditions, the insect remaining on the cotton plant only so long as the relative humidity is low.

The life cycle stages.

As is usually the case in Terebrantian thrip species, the life cycle comprises egg stage, first stage larva, second stage larva, prepupa, pupa and imago.

The morphology of these stages in the case of *Thrips tabaci* has been fully dealt with by Van Eecke (1922) and need not therefore be discussed here.

The following points however deserve to be briefly noted. The first point concerns the variability in colour of the adults and larvae. Second stage larvae vary in colour from milk white to orange yellow. Adults vary from light yellow to brownish black. These colour variations occur irrespective of the mean temperature or the mean humidity at which rearing is carried out, and there can be little doubt that they are not

associated with differences of temperature and humidity. In the case of the genus *Heliothrips* whose species habitually, in the adult stage, roam about on the surface of foliage exposed to tropical sunlight, the adult colouration is usually brown or black, but in the case of *Thrips tabaci*, although at times adults occur numerously on the upper surface of cotton leaves, careful observation did not support the possibility that dark coloured individuals tend to frequent the upper surface of leaves more than light coloured ones do.

The second point concerns the proportion of male to female individuals. The male of *Thrips tabaci* has been described by Hinds (1903) and by Van Eecke (1922) and is stated to be similar morphologically to the female, but smaller in size. In the present case, nearly 3000 individuals of the adult stage, collected at intervals throughout the summer of 1926, were examined without a single male individual being found. Possibly males are produced towards autumn, but reproduction throughout the summer must have been parthenogenetic.

Life cycle in the field.

The ovaries of *Thrips tabaci* consist of four tubules on each side; the tubules are short and panoistic.

The mature egg is bean shaped and is approximately 200 μ in length by 100 μ in breadth. The immature egg is small and the large nucleus is clearly visible, but as the egg matures it becomes heavily laden with yolk which obscures the internal structure. The yolk appears to consist of a mass of globules and is clearly visible through the chorion.

The eggs are laid singly, scattered over the under surface of the leaf, but imbedded in the mesophyll tissue. The process of egg laying is a long one as the ovipositor is inserted deeply in the leaf tissue. In one case, a female took at least 15 min. to deposit a single egg, and this thrips was not observed until after the ovipositor had been inserted. The eggs can be distinguished under a binocular microscope as translucent spots, especially if a leaf is dehydrated and soaked in oil of cloves; if the embryo is well advanced, the egg can be detected as a small projection of the leaf surface. The newly laid egg does not differ greatly from the mature ovarian egg but is slightly larger; during embryonic development, however, the egg loses its bean-like shape and becomes oval; the embryo can be seen through the chorion and as the time of hatching approaches, the red larval eyes become conspicuous.

The number of eggs laid by one female is probably not great. Hinds (1903) gives the number in the case of *Anaphothrips* as being 50 to 60,

and states that from 30 to 40 per cent. of these hatch. In *Thrips tabaci*, the number of eggs laid by one female is possibly about the same as with *Anaphothrips*, since 10 to 20 larvae are obtainable from an individual female.

In the glasshouse, at a mean temperature of 19° C. and a mean relative humidity of 84·5 per cent., the duration of the egg stage between oviposition and hatching averages 8 days. The larva forces its way head first out of the egg and through the slit made in the leaf surface by the ovipositor of the adult. It is approximately 0·37 mm. long, the colour is translucent white, and head and appendages are very large in proportion to the rest of the body. The larvae are at first somewhat gregarious in habit, and feed clustered together, generally in the shelter of the somewhat protruberant leaf veins; as they become older and larger, they scatter over the leaf surface in search of fresh food, but do not seem capable of migrating from one leaf to another.

The age at which the first moult occurs seems to vary considerably, and the larva may be comparatively large before it reaches the second stage.

The second stage larva is approximately 0·9 mm. long, almost as large as the adult; the colour varies from pale to deep yellow; head and appendages are only a little larger than those of the newly hatched larva.

Under the conditions of temperature and humidity stated above, the two larval stages last, together, between 10 and 14 days.

Full-fed larvae as a rule leave the plant, but whether by migration down the stem or by simply falling from the leaf, is not definitely settled. They bury themselves in the surface soil, moult and become prepupae. Exceptionally, the prepupa is found on the leaf, sometimes in empty cocoons of a species of *Aphidius*.

The prepupa is similar in size to the second stage larva. It does not feed but is capable of movement, although not inclined to move from place to place unless distrubed. The duration of this stage is short, between 1 and 2 days in this case.

The pupa is similar in habits to the prepupa but its duration is longer, lasting between 4 and 7 days.

Thus the life-cycle between oviposition and imaginal emergence under the glasshouse conditions described is 23–31 days; later in the summer, with a mean temperature of 15° C., the life-cycle is at least 35 days.

The number of generations between May and October in the glasshouse was seven.

The observations of other workers concerning the life-cycle of *Thrips tabaci* may be tabulated as follows:

Locality	Observer	Temp. (° C.)	Egg stage (days)	1st and 2nd larval stages	Prepupa and pupa	Total
Holland	Van Eecke	?	7	8	4 days	3–4 weeks
Massachusetts (glasshouse)	Hinds	?	4–7	7–8	7 „	3–4 „
Florida	Quaintance	?	3½–4	7–9	4 „	16 days
Iowa	Horsfall and Fenton	?	3–10	7–21	4–7 „	7 days (*sic*) to several weeks
Manchester (glasshouse)	MacGill	19	8	10–14	1–2, 4–7 „	4 weeks
		15	8–11	16–19	3–5, 8–12 „	5–6 weeks

Although no data as to mean temperatures and humidities have been given by other observers, it seems clear, from the variance of opinion concerning the duration of the several stages, that the total length of life-cycle of *Thrips tabaci* is prolonged or abbreviated by changes in temperature and humidity, and that this species is not an insect in whose life-cycle a curtailment or a prolongation of one stage can be compensated by a corresponding prolongation or curtailment of a succeeding stage, and so not an insect whose life-cycle remains constant as regards length throughout varying conditions of temperature and humidity.

Life-cycle at constant temperatures, and constant humidity.

Data concerning the duration of life-cycle stages in a constant saturated atmosphere and at constant temperatures, were obtained by using a Multiple Temperature Incubator, a simple type of that described by Williams (1924).

This consisted essentially (Fig. 2) of a copper hot-water chamber, 12 × 12 × 10 in. in dimensions, and a double walled zinc ice box of about the same size; the two boxes were connected by a 4 in. diameter tube of copper foil, nearly 6 ft. long, whose closed ends protruded each into one of the chambers. The temperature of the hot-water chamber was kept constantly at 63° C.; the ice box was replenished daily.

It must be noted that there was no passage of hot water along the tube, but by radiation of heat through the metal tube, a range of temperature, each constant within the limits of 1° C., was obtained along

the tube. In this case, the range of temperatures obtainable was from 7–50° C.

Along the tube was drilled a series of holes of $1\frac{1}{2}$ in. diameter, at equal intervals, in each of which a corked tube was placed. The copper tube with its contained tubes was insulated by being wrapped round and round with alternate layers of cotton wadding and asbestos mill-board. The hot-water chamber was similarly insulated. Each tube contained enough distilled water to ensure a saturated atmosphere and was large enough to hold a piece of fresh cotton leaf for the support of thrip stages. The particular points of temperature made use of are indicated in the figure.

Fig. 3 indicates the percentage of larvae reaching the prepupal stage, the percentage of prepupae reaching the pupal stage, and the percentage of pupae reaching the imaginal stage, at a constant humidity value of

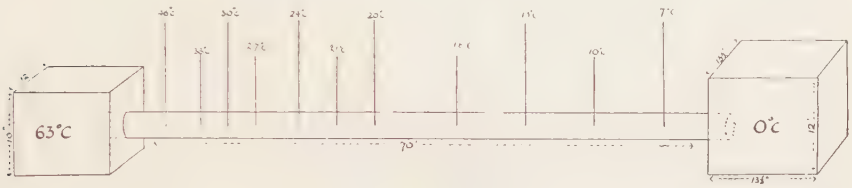

Fig. 2. Diagram to indicate dimensions and temperatures of the multiple temperature incubator.

100 per cent. of saturation, and at a number of temperature points between 7 and 47° C.

It will be noted from the curves that, in the case of larvae and pupae particularly, the temperature point at which the greatest percentage of individuals transformed into the next stage was 21° C. On either side of this temperature point, the percentages drop fairly regularly until, at each extreme of the scale, no adults hatched out.

At this temperature, 36·6 per cent. of larvae became prepupae, 95 per cent. of prepupae became pupae, and 91 per cent. of pupae became imagines. The great discrepancy between the number of larvae which failed to transform, and the numbers of prepupae and pupae which failed to do so, cannot be altogether attributed to loss during manipulation. Such loss did occur. The pieces of leaf in each tube had to be changed daily, and the minute stages had to be sought for and transferred with a fine brush. The 5 and 9 per cent. losses of prepupae and pupae are almost certainly wholly due to loss during manipulation. The reason for the fact that at temperatures of 7, 10, 13 and 16° C.,

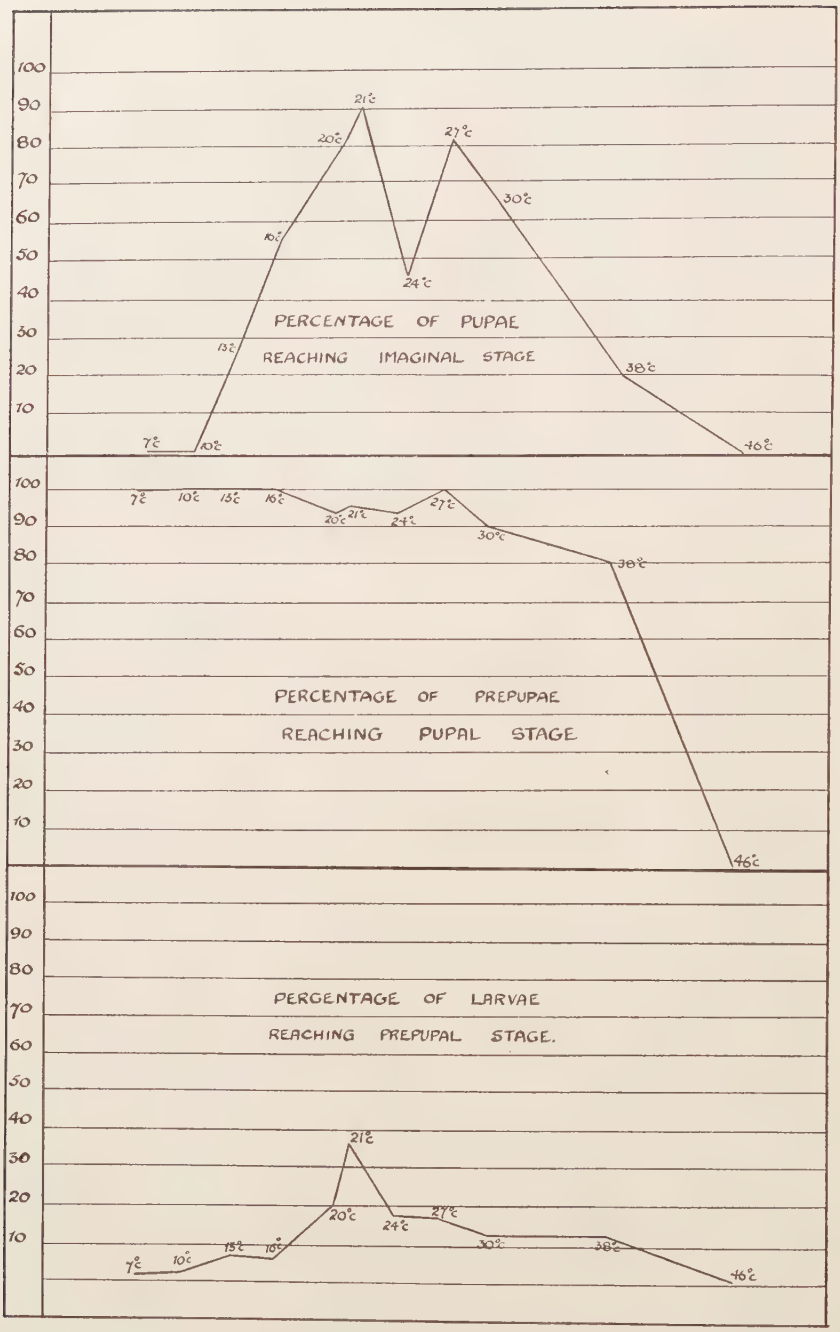

Fig. 3. The percentages of transformations from one stage to another at differing temperatures.

100 per cent. of prepupae became pupae supports this explanation, since at these temperatures so few pupae were obtained, that none were likely to be overlooked during transference.

The 66·6 per cent. loss of larvae cannot be attributed solely to loss during transference. Possibly the artificial conditions, absence of soil and so forth is the cause of so many larvae failing to transform. On the other hand, the occurrence of a high rate of larval mortality in the field seems indicated by the ratio of larvae to adults which occurred among the thousands of individuals counted during the series of leaf counts described in the previous part of this paper. This ratio was, for American cotton plants, 9 adults to 16 larvae; for Egyptian cotton plants it was 2 adults to 6 larvae; for *Cajanus indicus* it was 4 adults to 10 larvae.

Thus, in a saturated atmosphere, the percentage of larvae which go through to the imaginal stage is not high at any temperature point, but reaches its maximum at temperatures approximating to 21° C. At temperatures between 10 and 38° C., the percentage of prepupae and pupae which transform further is probably, excluding losses due to faulty experimental technique, absolute. The minimum effective temperature is below 7° C. and the maximum effective temperature is above 38° C.

The percentage of transformations at other degrees of relative humidity will be discussed in a later paper but such data as have already been obtained do not suggest that this percentage is higher at lower humidities than it is at saturation.

The larvae used in the incubator experiments were not very young, the majority being 3 to 4 days old, so that the duration values for larval stages, obtained by this method, are only approximate. At temperatures of 21° C. or higher, the maximum duration of a larval stage was 9 days, so that the total larval period was 12 to 13 days. At temperatures below 21° C., the maximum duration was 15 days, a total length of 18 or 19 days. The duration of prepupal and pupal stages increases greatly with fall of temperature. Thus:

Temperature ° C.	Average prepupal duration (days)	Average pupal duration (days)
38	1·44	2·2
30	1·22	2·3
27	2·0	4·4
24	2·5	4·0
21	2·0	3·7
20	2·1	4·8
16	3·1	8·0
13	5·1	12·6

It will be noted that temperatures below 21° C. appear to have a greater effect on the rate of development than do those above this.

At 38° C., the average prepupal duration is 1·44 days, and at 21° C., it is 2·0 days; that is to say, for a difference of 17 degrees of temperature there was only 0·56 of a day difference in the length of the stage. On the other hand, at 13° C., the average prepupal duration was 5·1 days, a difference from that at 21° C. of 3·1 days for a difference of 8° C.

Similarly, at 38° C., the pupal stage averaged 2·2 days, at 21° C., it averaged 3·7 days, at 13° C. it averaged 12·6 days. That is to say, there was a difference of only 1·5 days for 17 degrees of temperature difference above 21° C., and of nearly 9 days for the difference of 8–9° below 21° C.

That is to say, as with other biological processes, the rate of prepupal and pupal development of *Thrips tabaci* is greater at low temperatures than at high temperatures. Between the limits of minimum and maximum effective temperature, each degree rise of temperature is correlated with a shorter prepupal or pupal duration, but the quantity time by which the duration is shortened is not constant for each degree of temperature; it is a quantity which gradually diminishes as the temperature increases.

It may be pointed out that the work of Parker, J. R. on *Melanoplus atlantis*, as summarised by Chapman, R. N. (1926), suggests that the duration of an insect life-cycle stage, when subjected to a range of temperatures *varying* around a certain mean value, will be shorter than when subjected to constant exposure to that temperature value, so that life-cycle values obtained in laboratory experiments for constant temperatures values do not accurately represent life-cycle values at mean field temperatures.

Under laboratory conditions of constant temperature, there is considerable individual variation as regards the duration of life-cycle stages. Thus, at 38° C., although the majority of prepupal *Thrips tabaci* only lasted between 1 and 2 days, three individuals had a duration of 2 days, and two individuals had one of 3 days. At 27° C., though most of the prepupae transformed after a period of between 1 and 2 days, one abnormal insect had a prepupal stage of 8 days.

At 21° C., about one-half of the prepupae transformed between 2 and 3 days, but cases of a prepupal stage lasting 3 or 4 days were common. At 16° C., whereas the majority of prepupae lasted between 3 and 4 days, one individual pupated after only 1 day. At 13° C., the minimum duration of a prepupal stage was 2 days, and the

maximum was 10 days; the majority however went five or more days before pupation.

The pupal stage showed even more variation in length than the prepupal one. The shortest time on record was 1 day, and a few individuals with this very brief pupal stage were found at all temperatures between 27° and 38° C.; no pupal stage lasted a shorter time than 3 days at 24° C., but at 21° C. there was one 1 day pupa, and several 2 day pupae. The longest pupal stage at temperatures above 21° was 10 days at 27°, and it is interesting to note that the longest prepupal stage, in a different individual, for hyper-optimum temperatures, also occurred at this temperature. Below 21°, the length of the pupal stage increased rapidly with fall of temperature; at 20° there was one 2 day pupa, but the majority lasted 5 or 6 days; at 13°, a length of 17 days was recorded for one pupa.

Thus, although the rate of development in *Thrips tabaci* tends to increase with rise of temperature, there is considerable individual variation.

In the list of acknowledgments already given in the previous part of this paper, I would stress particularly the names of Mr H. Britten for help in the identification of various insect species, and Mr V. P. Walley, Chief Inspector of the Gezira Research Farm, Sudan, for information concerning meteorological data for that locality.

SUMMARY.

1. The life-cycle of *Thrips tabaci* from oviposition to imaginal emergence, on cotton plants, under conditions of temperature varying between a mean maximum of 26·7° C. and a mean minimum of 11·25° C., and of relative humidity varying between a mean maximum of 92·4 per cent. and a mean minimum of 74·7 per cent., has a duration of 23–31 days, comprising an egg stage of 8 days, two larval stages with a combined duration of 10 to 14 days, a prepupal stage of 1 to 2 days and a pupal stage of 4 to 7 days.

2. Under laboratory conditions, in a constant saturated atmosphere, the percentage of larvae which transform into prepupae is not high at any temperature but reaches a maximum of 33·4 per cent. at temperatures near 21° C. The minimum effective temperature is below 7° and the maximum effective temperature is above 38°.

3. The high larval mortality is not wholly due to faulty technique,

nor to the saturated atmosphere, nor to the artificial conditions. A similar high rate of mortality is believed to occur under field conditions.

4. The percentages of prepupae and pupae which transform are high at all temperatures between the minimum and maximum effective points, and would probably be absolute under conditions of perfect technique.

5. The length of the life-cycle is decreased by increase of temperature. The average times of development plotted against temperature give, with minor corrections, an hyperbola similar to the developmental curves given by Krogh.

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(*Received* 24*th June,* 1927.)

THE BIOLOGY OF THYSANOPTERA WITH REFERENCE TO THE COTTON PLANT

3. THE RELATION BETWEEN FEEDING HABITS AND PLANT LESIONS

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(With 8 Text-figures.)

The part played by the mouthpart components of Thysanoptera, and in particular of foliage feeding Terebrantia, in producing the characteristic lesions shown by an attacked plant, and the histological nature of the lesions, are points concerning which a certain vagueness appears to exist among students of the group.

Despite the fact that the foliage lesions produced by different species of thrips do not differ greatly in type, and that there is little difference between the mouthparts of different Terebrantian species, somewhat varying explanations have been put forward.

Thus the thrips has been stated to puncture the tissues and drain the contents of the cells, causing the cell walls to collapse (Horton, J. R. 1921, re *Scirtothrips citri*. Moul.); to pierce the epidermis and rasp away the leaf tissues within (Russell, H. M. 1912, re *Heliothrips rubrocinctus* Giard.); to rasp the leaf tissues and suck up the sap as it exudes (Bedford, H. W. 1921, re *Heliothrips indicus* Bagn.); to pierce the vegetable tissue with its stylets and suck up the liberated plant juices (Cameron, A. E. and Treherne, R. C. 1918, re *Taeniothrips inconsequens* Uzel).

The experiments and observations recorded in this paper were carried out with *Thrips tabaci* under glasshouse conditions. The suitability of this species for experiments, the chief features of its life-cycle, and the degree to which it may infest the cotton plant, have already been discussed in previous papers. The plants used as host plants were cotton (*Gossypium* sp.), *Cajanus indicus* (pigeon pea, ads sudani), *Dolichos lablab* (field beans, lubia), *Hibiscus esculentus* (bamia) and *Calotropis procera* (Sodom's Apple, ushr), all grown from seed obtained in the cotton growing districts of the Sudan.

The varieties of cotton plant used were two Egyptian varieties Sakellarides and Maarad, two long staple American Upland varieties namely Webber and Cleveland Big Boll, and an unidentified short staple variety of Indian cotton.

Of these plants, the most susceptible of the cotton varieties was the Indian; then came Webber, which had, throughout the season, a mean degree of infestation approximating to 9 adults or to 16 larvae per 100 sq. cm. of leaf surface. Cleveland was less susceptible than Webber. The Egyptian varieties were less susceptible still, the mean numbers of adults and larvae per 100 sq. cm. of leaf surface, throughout the summer, being approximately two and six respectively.

Of the other plants, *Hibiscus esculentus* was almost unattacked. The leaves of this plant are very hairy and the lower surface of the leaf is covered with minute spherical exudations of numerous glands. *Dolichos lablab* was liable to slight attack when young. *Calotropis procera*, the poisonous ushr of the North African deserts, was also attacked only when young. *Cajanus indicus*, a plant that is not attacked in the Sudan by *Heliothrips indicus* and is used as a protective hedge along the windward edges of the cotton fields, was attacked freely by *Thrips tabaci*, the mean numbers of adults and larvae per 100 sq. cm. of leaf surface, throughout the period, being approximately four and ten respectively.

The parts of the plant attacked.

In the case of cotton plants, *Thrips tabaci* infests the lower surface of the leaves particularly. Both adults and larvae are negatively phototropic and oviposition occurs almost invariably in the tissues of the lower surface of the leaf. The adults are slightly migratory but larvae do not leave the leaf they are born on, until they make their geotropic migration to pupate in the soil. When the lower surface of a leaf has been severely damaged and is crowded with thrip stages, some adults and larvae will migrate on to the upper surface, especially when the leaf is shaded by others, or when the sky is cloudy, or possibly in the night. Such upper surface individuals, however, are always very restless.

The preference shown for the lower surface of foliage is probably concerned with differences in epidermal thickness, between the two surfaces, rather than a question of phototropism. In cotton leaves, the difference is slight so that larvae can feed on the upper surface, but the habit has become established as an adaptation to other food plants in which this difference is more pronounced.

In the case of *Cajanus*, the usual feeding surface is the upper one,

but again thrips will occur on the other surface when crowded off the upper one. *Cajanus* is a somewhat bushy plant and the thrips frequent chiefly the lower, well-shaded leaves.

Only the leaves of the cotton plant are attacked as a rule; the bracts surrounding the boll are attacked in a few cases, and exceptionally, the bolls themselves are attacked. On American plants, the favourite situation of feeding adults and larvae is the area where the petiole joins the leaf. On Egyptian plants, the leaf edges, the area along the main veins, and the area around the marginal indentations, are all equally favoured. Both adults and larvae show a tendency to keep in the shade of the prominant veins.

Larvae occur in greater numbers on the lower, older leaves; adults are most numerous on the upper, younger leaves. Very rusty and partially withered leaves, and very young leaves, are usually free from thrips. The explanation of the latter fact is probably that such young leaves are put forth near the tip of the plant, and as infestation proceeds upwards and a normal thrip life-cycle is 3 to 4 weeks, such leaves have had time to grow considerably before the adults spread upwards to them. In severely attacked plants, where much leaf shedding has occurred, young leaves are produced low down on the stem and are then quite freely attacked.

The mouthparts.

The mouthparts of various other species of Terebrantian thrips have been described in detail by numerous workers, notably by Jordan (1888), Garman (1890), Bohls (1891), Buffa (1898), Borden (1915), Peterson (1915), Reyne (1926), and as a careful examination of the mouthparts of *Thrips tabaci* has not disclosed the existence of any fundamental points of difference between this species and those described by the workers listed above, it will be sufficient here to limit description to certain features whose understanding is necessary to the explanation of the mode of operation of the mouthparts.

The mouthparts are bent backwards underneath the head and form a short conical proboscis or *mouthcone* (Figs. 1 and 8). This cone is directed at an angle of 45 degrees to the longitudinal axis of the body. The front of the cone is composed of a *clypeus* and *labrum* separated somewhat from one another by a membrane. Both clypeus and labrum are asymmetrical. Their shape and component sclerites are shown in Fig. 1. Each side of the mouthcone is formed by a triangular structure generally

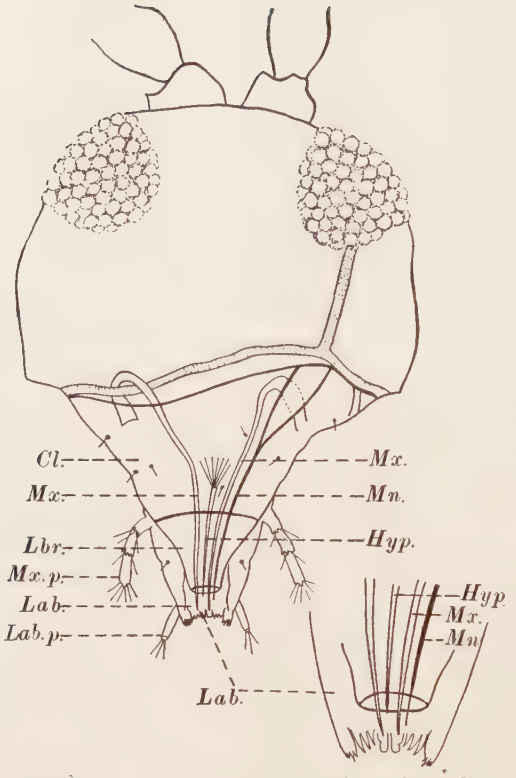

Fig. 1. Head of *Thrips tabaci*. × 700. *Cl.*, clypeus; *Hyp.*, hypopharynx; *Lab.*, labium. *Lab.p.*, labial palps; *Lbr.*, labrum; *Mn.*, mandible; *Mx.*, maxilla; *Mx.p.*, maxillary palp.

Fig. 2. Labium of *Thrips tabaci*. × 1600.

regarded as the galeal portion of the maxilla since it carries a three-jointed palp (Fig. 3).

The rear wall of the cone is constituted by the triangular *labium*, whose appearance is shown in Fig. 2, bearing near its tip a pair of two-jointed palps. The labium is longer than the labrum and maxillae, and projects beyond them as a flexible, somewhat fleshy flap. It may be noted that the tips of the maxillae and of the labium are provided with

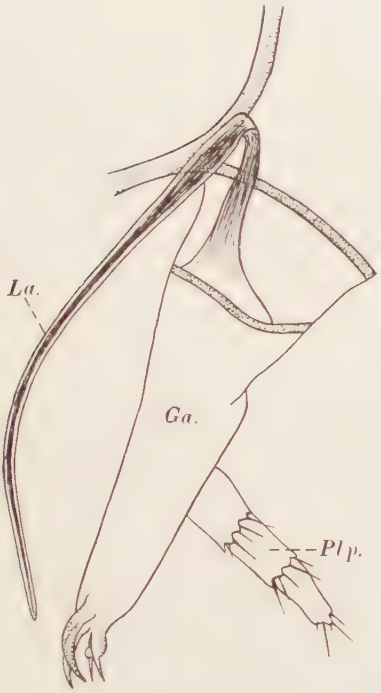

Fig. 3. Left maxilla of *Thrips tabaci*. × 1600. *Ga.*, galea; *La.*, lacinia; *Plp.*, palp.

Fig. 4. Mandible of *Thrips tabaci*. × 1600.

hooks, possibly in order that this part of the mouthcone rim can grip closely the leaf surface.

The actual piercing organs comprise four *stylets* or lancets, the *paired stylets*, the *median stylet*, and the *left stylet*.

There is considerable controversy as to the homologies of these stylets. With this controversy we are not concerned. It is sufficient here to adopt the view of Reyne, the most recent investigator, and regard

the paired stylets as maxillary laciniae, the median one as the hypopharynx, and the left one as the mandible.

The shape and dimensions of these stylets may be gathered from the figures.

The method of using these stylets will be discussed later.

The morphological appearance of the plant lesions.

The gradual changes in the appearance of a leaf which has been attacked by *Thrips tabaci* may for convenience be separated into four stages (Fig. 5).

Stage 1. The under surface of the leaf shows a number of tiny, scattered areas which have a varnished, shining appearance, as if drops of gum arabic had coagulated on the leaf. No epidermal damage is apparent even under the microscope but each patch has a frothy, blistered appearance with interference colours. The glistening appearance is not due to a deposit on the cuticle as it cannot be removed by the action of such solvents as alcohol, ether, chloroform or xylol, nor by scraping, unless such treatment destroys the epidermis. That is to say, the shining patches do not represent a hardened exudation of sap or of insect saliva, but are due to cellular change beneath the epidermis.

Further, the appearance cannot be artificially reproduced by pricking or scraping the epidermis, nor by pricking followed by a stay of some hours in a vacuum chamber. That is to say, the assertion by Williams that, in the case of peas attacked by the Pea Thrips, the "silvering" is due to air in the outer cell layers of the plant let in by the sucking of the larva, is not wholly true, at any rate for *Thrips tabaci*. Some other cellular change in addition to the entrance of air is required.

Stage 1 damage is associated particularly with the presence of adults, and may occur often on the upper surface of leaves where neither adults nor larvae are present. In such cases, however, it is certain that the leaf surface has been visited by an adult thrips.

Stage 2. Within 24–48 hours the patches take on a greenish brown colour and become much more conspicuous.

Stage 3. The brown spots become larger, more scattered over the leaf surface, particularly occurring along the course of the main veins. With Egyptian plants, these patches are pale brown and more frequently found on the upper leaf surface than in the case of American plants. If pieces of the damaged leaf at either Stages 2 and 3 be taken, soaked in an oxydising agent such as nitric acid plus potassium chlorate, or sodium hypochlorite, and, when transparent, transferred to cold water,

Fig. 5. Leaves of Sakellarides cotton showing Stage 3 and Stage 4 damage by thrips.

it is possible to remove the piece of epidermis over the damaged area. To such pieces of epidermis the superficial layer of mesophyll cells will adhere at the points of damage but not elsewhere. Such pieces can be conveniently stained with Bismarck brown.

Careful examination of such pieces under a high power binocular microscope reveals nothing in the nature of punctures, but shows a number of gashes in the damaged areas, each gash within the boundaries of a single epidermal cell (Fig. 6).

Around each gash, the epidermal cells are intact but cover a little patch of somewhat disorganised mesophyll cells.

There is little doubt that the brown appearance of the patches in a Stage 2 or Stage 3 leaf is due to necrosis of the more superficial mesophyll layers, and that these brown patches underlie the epidermis. It is the lens-like effect of the transparent epidermis overlying a patch of

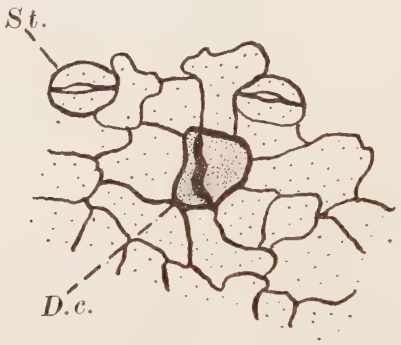

Fig. 6. Portion of epidermis from lower surface of a cotton leaf, to show the appearance of a cell gashed by a thrips. × 700. *St.*, a stoma; *D.c.*, damaged cell.

shattered mesophyll cells that produces the glistening, colour-fringed effect of Stage 1 damage.

Necrosis is probably a purely mechanical sequel to insect damage, and not aided by any toxic salivary secretion. Similar brown patches can be produced, but not glistening patches, by pricking the epidermis with a sterile needle. They can be produced by pricking with a sterile needle which has been dipped in an infusion of damaged leaves made by grinding up such leaves with sterile sand and distilled water. In neither case does damage spread beyond the little patch of dead mesophyll cells which results in the neighbourhood of the puncture.

Similar spots produced by an isolated adult are a little larger than the artificially produced ones but again do not spread greatly in area, whereas, if the salivary secretion of the insect were toxic, one would

expect extensive spreading of the damaged spot even after the insect had been removed. Actually, only when several insects are allowed to roam about the leaf for some time, can one obtain spots sufficiently close together to merge into brownish areas.

In this case, the merging of the spots is aided by a general necrosis of the leaf caused by interference with transpiratory and photosynthetic functions.

Stage 4. The patches tend to run into one another so that the under surface of the leaf becomes uniformly purplish or rusty brown. On Egyptian leaves, the colour is a light brown and the veins are bordered by reddish brown patches. The upper surface of the leaf becomes dry, harsh and wrinkled. The Stage 4 leaf in fact is with difficulty distinguishable, as regards colour changes, from a normal dying or dead leaf. Necrosis however has involved the epidermal cells and these are broken and shapeless. Thrips occur rarely on Stage 4 leaves.

The rapidity with which Stage 4 is reached after initial infection, depends upon the degree of infestation to which the leaf has been subjected. The usual length of time in the case of American leaves was ten days. A large number of experiments were made in the confinement of known numbers of adults or larvae upon leaves for varying intervals of time, upon marked and isolated leaves. The results obtained indicated:

(*a*) That one thrips alone can bring about Stage 1 damage.

(*b*) That if no further feeding upon the leaf is allowed, the leaf being segregated so far as possible by removal of all leaves in its vicinity, damage does not proceed beyond Stage 2.

(*c*) That only when the attack is cumulative and severe, does the leaf assume the appearance of Stages 3 and 4.

Presumably when only a few cells are tapped, necrosis of the leaf does not proceed beyond the damaged points and premature falling of the leaf does not occur. If a large number of cells are tapped, however, the whole leaf becomes uniformly withered and leaf shedding occurs long before the leaf would normally fall.

It is probable however that different varieties of the cotton plant will vary as regards susceptibility to thrip injury. Reyne (1921) states that there is great difference in behaviour of food plants with regard to the injury caused by the Cacao Thrips (*Heliothrips rubrocinctus*); in Cacao, *Mangifera*, *Anacardium*, necrosis of the feeding marks occurs and the leaves are cast; in this case severe damage is done as the trees soon become exhausted by accelerated change of leaf; in others (*Ter-*

minalia, *Bixa*), the leaf tissue does not die and premature leaf shedding does not occur.

Damage is produced by both adult and larval *Thrips tabaci*. Leaves on which only larvae were confined deteriorate much more slowly than those upon which adults only are confined. The latter leaves pass rapidly into Stage 2 and reach Stage 3 whilst the former leaves are only slowly approaching Stage 2. The appearance of the damage produced by adults is indistinguishable from that produced by larvae.

The histology of the lesions.

Pieces of leaf were fixed in weak Fleming's solution; fixation was carried out in partial vacuo, as described by other workers. The results with cotton leaves are not so satisfactory as those obtained by fixation with Carnoy's fluid.

Sections of thickness 10 μ to 12 μ, and 18 μ to 20 μ, were cut; the thicker sections were more reliable for purposes of examination. Of a large range of stains and combinations of stains used, the most satisfactory results were obtained with iron haematoxylin, and with aniline blue and cotton red in combination. Bismarck brown was used for staining portions of epidermis or cuticle. Sections were cut from three classes of material, namely:

(i) fresh undamaged leaves and normal withered leaves,

(ii) leaves in the four stages of thrip damage,

(iii) leaves on which known numbers of thrips had been confined for known periods of time.

The conclusions derived from examination of several thousands of such sections may be summarised as follows (Fig. 7):

Stage 1. The epidermis is intact on both sides, except for short breaks in the lower epidermis. There is no evidence of punctures such as Reyne (1926) claims are visible in the epidermis of leaves of Liberian coffee attacked by *Heliothrips haemorrhoidalis*. Below the epidermal breaks, and below intact portions of the epidermis, where the section has possibly passed to one side of a break, there is slight disorganisation of the outermost mesophyll layer, some of whose cells appear to be shattered and emptied, and an unusually large number of air spaces. The palisade layer is always intact.

Stage 2. The appearance of this stage is similar to that of Stage 1, but cells of the lower epidermis are in places somewhat misshapen. Distortion of patches of the outermost mesophyll layer is still more

obvious and large spaces occur where the cells are destroyed or emptied and more or less shrivelled.

Stage 3. The whole section has a shrivelled appearance. The mesophyll is so disorganised as to appear almost unrecognisable in places. Disorganisation has spread also to the palisade tissue but the upper epidermis is still fairly intact.

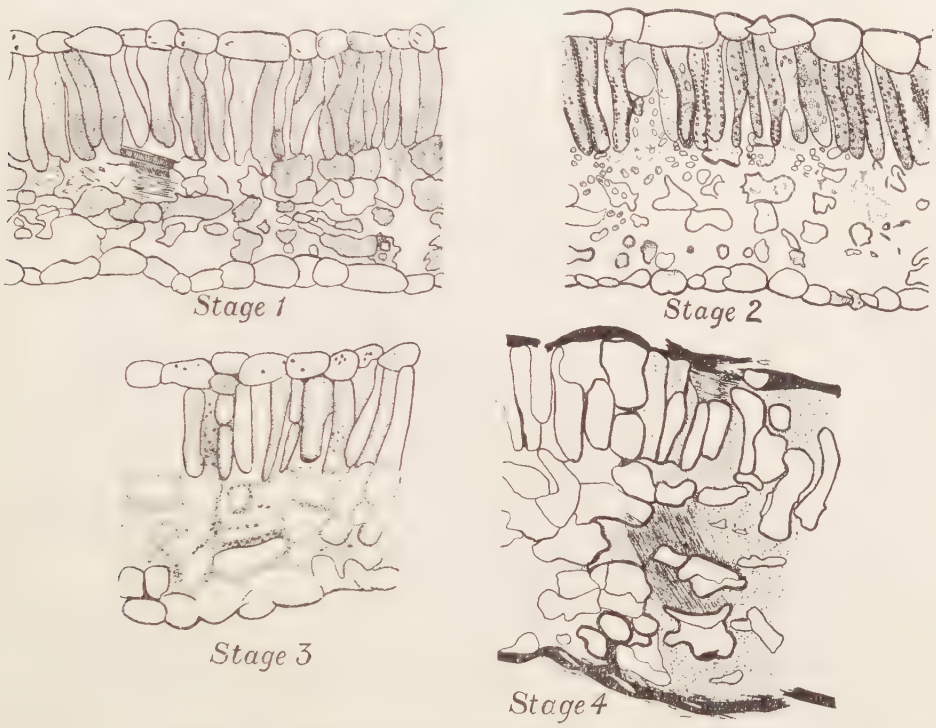

Fig. 7. Histological appearance of the four stages of thrip damage to cotton leaves. × 500.

Stage 4. All the tissues are disorganised. The mesophyll is completely broken down. Only the outlines of the palisade layer remain. Both epidermal layers are broken down.

That is to say, the histological appearance of damaged leaves suggests that the damage caused is of a purely mechanical nature. The appearance of Stage 4 leaves is in no way different from that of undamaged leaves which have gradually withered.

The histological appearance of leaves upon which adults or larvae had been separately confined differed in no way from one another.

Conclusions concerning relation between the mode of feeding and the leaf lesions.

The following conclusions are based upon close observation of feeding adults and larvae, microscope examination of the mouthparts of adult and larval stages, and microscopical examination of damaged leaves. The method used by some workers when studying the feeding habits of Hemipterous insects, of fixing the feeding insect to the leaf by a drop of wax and then preparing insect and piece of leaf for section cutting, was tried with *Thrips tabaci* but was found useless. The mouthparts do not penetrate sufficiently deeply into the leaf tissues to ensure that the insect will remain in position after the wax has become dissolved by the fixative. Despite the greatest care in the subsequent technique, it was not possible to keep a single specimen in position, although perfectly easy to anchor an ovipositing adult by the ovipositor.

Cotton leaves vary of course in thickness with age, size, variety, and water supply. The proportions of the various histological layers to one another, however, may be indicated by the following measurements which represent means of a large number of leaf measurements. When the mean thickness of the leaf is 143 μ, the upper epidermis is 17 μ, the palisade tissue 54 μ, the mesophyll layers 61 μ, the lower epidermis 11 μ, respectively. The lower mesophyll layers are somewhat loosely packed, a feature which varies considerably in different varieties of the cotton plant, and appears also to vary according to the intensity of light to which the leaf happens to have been subjected.

On the lower surface occur numerous hairs. There is no evidence that the presence of such hairs is repellent to thrips. The spacing between the hairs is sufficiently wide to permit such minute insects as Thysanoptera to move about freely. In fact the hairy Indian and American plants were more infested than were the smoother leaved Egyptian plants. It is possible however that the closer spacing of the fine hairs on the lower surface of *Cajanus* leaves is a factor in producing the relative freedom of this surface from thrip attack.

The method of feeding appears to be as follows:

The mouth cone is applied firmly to the leaf surface, the animal sinking somewhat between the anterior legs so that the abdomen is tilted upwards. The hooked tips of maxillae and labium grip the leaf surface firmly, but since the rear wall of the cone is longer than the fore wall, and flexible, a slight rocking movement of the head is still possible. The stylets, at any rate the maxillae and the mandible, can be protruded apparently through a circular rim at the tip of the labrum.

The distance to which they can be protruded is not easy to estimate, since in microscopical preparations there is the possibility that pressure on the cone has brought about abnormal length of protrusion. In the case of *Thrips tabaci*, the distance to which the stylets can be protruded beyond the labral rim appears to be approximately 11 μ for the mandible, and 27 μ for the maxillae. Whether the hypopharynx can be protruded also is uncertain. Borden claims so, for *Heliothrips haemorrhoidalis*, and possibly such is also the case with *Thrips tabaci*.

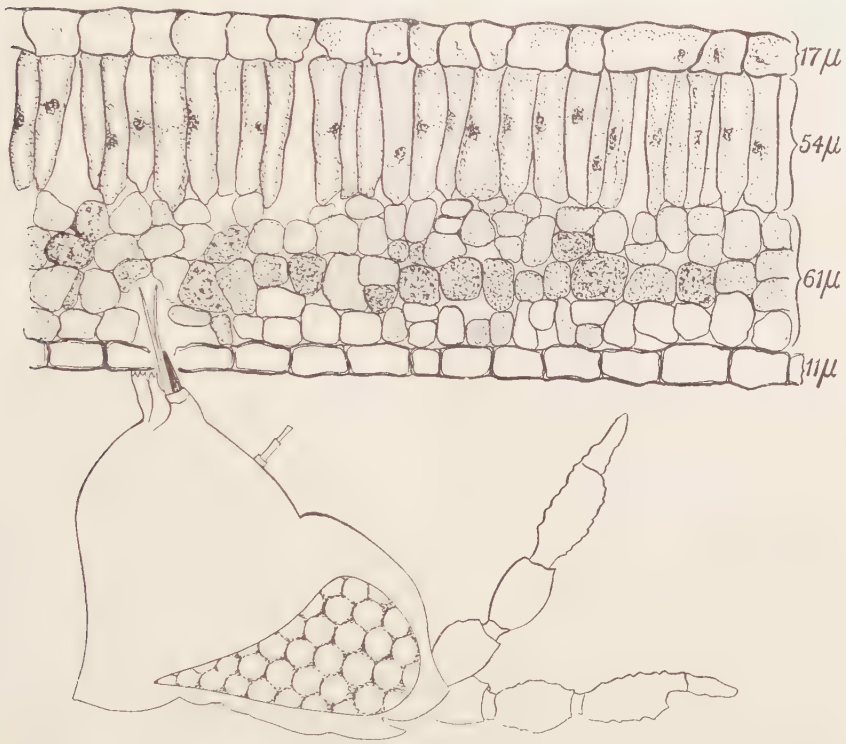

Fig. 8. Diagram of the head of a feeding thrips to indicate its size relative to the leaf tissues, and the depth to which maxillae and mandible are inserted.

What exactly occurs, during feeding, within the semi-enclosed chamber formed by apposition of the mouth cone to the leaf surface, is difficult to follow, but seems to be somewhat as follows.

The feeding thrips commences to swing the head slightly upwards and downwards, the flexibility of the labium permitting this to occur without disturbance of the position of maxillae and labium. The rocking

movement is made possible by the triangular shape of the head (Fig. 8). At each swing upwards, when the thrips is on the lower surface of the leaf, as in the figure, the mandible is protruded, at each swing downwards it is withdrawn; the insect thus uses the mandible as a man uses a pickaxe, and its chief function appears to be that of breaking through cuticle and outer epidermal wall. That is to say, it gashes or tears rather than pierces. The arc subtended by the angle of swing is limited by the degree of flexibility of the labium. It is in any case small, since the gash is within the length of an epidermal cell, that is to say within a length of 50 μ, although in some cases it may cut across the dividing wall between two cells. The protruded mandible will in most cases not be long enough to reach the lower wall of the epidermis. When the upper surface is broken through, the longer and weaker maxillae come into play, the head swings lessen somewhat, and the boundary between epidermis and outermost mesophyll layer is broken down. Probably the lateral boundary walls of a number of mesophyll cells are broken down, since these cells are smaller than those of the epidermis, and a number of them will underlie one epidermal cell.

There is no evidence that the mouth cone is pushed down into the gash thus created, or that it can be pushed down into a stoma and the leaf tissues attacked that way. The rocking movements, essential apparently to the use of the stylets, would be impossible if the cone became wedged into a gash or into a stoma. The feeding habits of the insect will be determined by the length to which it can protrude its stylets, and the epidermal thickness of host plants. The variation in susceptibility of individuals in a block of plants of the one variety, ranging as it does from very slight injury to severe injury, will arise almost entirely through variations in epidermal thickness between leaves of different plants, and in variations in age and size of the thrip stages on the plants.

After the gash is made, the head movements cease and the thrip remains apparently motionless, absorbed in the effort of sucking inwards the chloroplasts of one or more mesophyll cells. The passage of chloroplasts into the pharynx is aided by the partial vacuum created in the closely applied mouth cone. Usually, after gashing one epidermal cell and absorbing the contents of the underlying mesophyll cells, the insect travels on and gashes another cell further away, following usually the course of a venule.

At first, the wound shows on the leaf as a glistening spot, the effect being due to the lens-like effect of the transparent epidermis over the empty patch of mesophyll cells underlying the gash. Then, as the patch

of mesophyll undergoes necrosis, the spot turns brown. Slight spreading of the necrosed spots, and the confluence of a large number of these spots, produces the Stage 3 damage. Gradual death of the injured leaf brings about the appearance of Stage 4.

To the list of acknowledgments already given in the first part of this paper, we would add the following names: Mr C. C. Brooks for very great help in the preparation of thrip mouthparts; Mr Howarth, Mr Walton and Mr Sutton of the Botanical Department staff of this University, and Dr K. Smith of the Agricultural staff, for advice concerning botanical technique.

Summary.

1. Observations and experiments concerning *Thrips tabaci* on cotton and other plants suggest that plant injury from thrip attack is in this case due entirely to premature and excessive defoliation, and is dependent in extent and severity upon the value of the infestation factor, or number of thrip stages per unit area of foliage surface. Differences between plant species, plant varieties and plant individuals as regards susceptibility to injury arise chiefly through variations in thickness of the epidermal cell layer.

2. Leaf injury consists essentially of necrosis of a patch of mesophyll cells lying immediately below a gash in an epidermal cell. Such necrosed patches are scattered and isolated when the infestation factor is low, but are confluent and form extensive rusty areas when the infestation is high. Such areas consist of dead cells of the superficial mesophyll layers; the deeper layers, palisade tissue and epidermal layers remain intact, except for the initial gashes made in epidermal cells. In later stages of leaf injury, such necrosis involves the whole leaf, all the layers become disorganised, and premature shedding occurs. There is no evidence that the insect salivary secretion is toxic.

3. The insect does not puncture or rasp the epidermis but gashes an epidermal cell by pickaxe-like movements of the single mandible, induced by a slight rocking movement of the head. In most cases, the mandible can only gash the outer epidermal wall, the inner wall and the lateral walls of the mesophyll cells being broken down by similar movements of the longer protruded maxillary laciniae. There is no evidence of attack through the stomata. Suction of the chloroplasts into the pharynx is aided probably by the partial vacuum established within the mouth cone when applied closely to the leaf surface.

4. The preference shown by thrip stages for the lower surface of leaves is believed to be due rather to differences in thickness of epidermis between the lower surface and the upper surface, than to negative phototropism. In plants where such differences are slight, such as cotton plants, thrip stages readily invade the upper leaf surface. On *Cajanus indicus*, the upper surface is the more favoured, the lower surface being unsuitable owing to the close spacing of numerous fine hairs. The more widely spaced hairs on cotton leaves do not act as a deterrent, the hairy American and Indian varieties being more heavily attacked than the smoother leaved Egyptian varieties of cotton.

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(*Received 24th June*, 1927.)

PROCEEDINGS OF THE ASSOCIATION OF ECONOMIC BIOLOGISTS

ORDINARY meeting held at 2.30 p.m. on May 13th, 1927, in the Imperial College of Science. The President, Mr J. C. F. FRYER, M.A., in the Chair.

DISCUSSION ON PLANT ALKALOIDS.

I. "The Principal Plants yielding Alkaloids" by Lieut.-Colonel A. T. GAGE, C.I.E., lately Director, Botanical Survey of India, and Superintendent, Royal Botanic Gardens, Calcutta.

II. "The Biochemistry of the Alkaloids" by Dr T. A. HENRY, Director, The Wellcome Chemical Research Laboratories.

III. "The Medical Aspects of the Alkaloids" by Dr J. TREVAN, The Wellcome Physiological Research Laboratories.

IV. General Discussion—Mr FRYER, Dr PETHYBRIDGE, Mr HOWES, Dr HENRY, Dr TREVAN.

I. THE PRINCIPAL PLANTS YIELDING ALKALOIDS.

BY Lieut.-Colonel A. T. GAGE, C.I.E., M.A., M.B., B.Sc.

(*Late Director, Botanical Survey of India, and Superintendent, Royal Botanic Gardens, Calcutta.*)

MAJOR CHIPP in his letter in which he conveyed his honourable invitation for me to take part in this alkaloidal symposium had the following remark: "We should not trespass on your time for more than twenty minutes." In this there was an obvious transposition of the pronouns, for he should have written "You should not trespass on our time for more than twenty minutes." Anyhow I hope I shall not much exceed that limit.

Fortunately for you and me I am not called upon to say anything about alkaloids themselves. I am merely the showman pointing to the pictures with more or less appropriate patter, to whet your appetite for the real performance, when Drs Henry and Trevan put their trained troupe of alkaloids through their paces.

I may just confide in you my personal impression of the rarity of alkaloids in their unadorned beauty. We consume incredible quantities of tea, coffee and tobacco, but how many of us have ever seen Caffeine or Nicotine. For half of every year for many years I lived amidst miles of Tea and Cinchona plants, but only on one occasion have I been introduced to Caffeine and Quinine, when the Government Quinologist showed me two phials, one of which, he said, contained Caffeine from tea-prunings and the other Quinine. I inspected them with the reverential care they seemed to call for and handed them back to him. Since then I have seen no other.

As within the time at our disposal only a limited number of the regiment of alkaloid-yielding plants can be inspected, the selection of those to file past leaves

room for difference of opinion according as to whether the arranger of the inspection is an economic biologist, a pure chemist, a pharmacologist, a physiologist, a physician, a grocer, a tobacconist or an artist in poisoning.

Although it is possible that not all of these are represented here, there is probably enough of different interests to make the selection somewhat of a problem. Being unfortunately precluded from adopting one of the bright modern methods of simultaneously raising money and gaining information by inviting you to participate on the usual terms in an "Alkaloid Ballot," I have fallen back upon a method of the B.B.C. who occasionally broadcast a programme arranged by an outsider according to his individual taste. So as one who is, or rather was, a mere systematic botanist, I have made out my own list with an equitable disregard of everyone else's interest. The question of the relative importance of alkaloids is as far as I am concerned evaded by passing the plants along in the order of the natural families to which they belong. At the risk of trespassing on Dr Henry's province, it may be mentioned here that when, as the slides are passing along, only one alkaloid is mentioned in connection with a plant it is not to be inferred that the plant contains no others. Further, when roots, seeds, bark or other parts are mentioned as the source of alkaloids, it means merely that the alkaloids are usually or most conveniently extracted from such parts. Finally such expressions as root or seed or bark and suchlike are extremely crude indications of how the protoplasm of a plant disposes of the alkaloids it produces in the course of its metabolism.

Lantern slides were then shown of the following plants, the lecturer commenting upon each.

1. ACONITUM NAPELLUS L. (Ranunculaceae), the familiar Monkshood of our gardens, is taken as the representative of a genus widely distributed over the Northern Temperate Zone. Most of the species store alkaloids, chiefly in the root, and several of these alkaloids are very poisonous. The typical alkaloid is Aconitine.

2. BERBERIS ARISTATA DC. (Berberidaceae) is a spiny evergreen shrub, a native of the Himalayas and the hills of Southern India and Ceylon and cultivated in this country as an ornamental shrub. The thin brittle root-bark more particularly yields *Berberin*, an alkaloid that occurs in a considerable number of other species, some belonging to the same genus, and others to different families.

3. PAPAVER SOMNIFERUM L. (Papaveraceae), the opium poppy, is probably a native of S.E. Europe and Asia Minor, but cultivated in Asia Minor, Persia, India still to a small extent, and China. The milky juice, which is collected by incising the capsules, is a fount of different alkaloids, over a dozen occurring in the stream. The chief one is of course Morphine.

4. CAMELLIA THEA (Ternstroemiaceae). The tea plant is native to Assam and extensively cultivated in that province, the Eastern Himalayas, Southern India, Ceylon, Java, China and elsewhere in the Tropics and Sub-tropics. It contains the most widely consumed of all alkaloids in the form of caffeine, which is usually extracted from the leaves.

5. THEOBROMA CACAO L. (Sterculiaceae). The cocoa plant is a small tree, a native of the northern parts of South America and up to as far north as Mexico. Extensively

cultivated in the tropics. The alkaloid Theobromine is the substance in the seeds which, along with the concrete oil, gives the flavour to the beverages that Linnaeus considered such divine liquors that he called the genus Theobroma, the Food of the Gods.

6. ERYTHROXYLON COCA Lamk. (Linaceae), the source of Cocaine, is a shrub extensively cultivated in the northern Andes and also in Brazil and other South American countries. The alkaloid that is extracted from the leaves reminds me that I might have included detectives in the list of the interested ones, as it is probably better known by repute than any other alkaloid to the ordinary man from its association with Sherlock Holmes in literature and Scotland Yard in newspaper reports of the activities of "snow" smugglers.

7. PILOCARPUS PINNATIFOLIUS Lemaire (Rutaceae), from the leaves of which the alkaloid Pilocarpine is obtained, is a shrub of Brazil. The leaves are compound, a foot or more long, with 2–5 pairs of 3–4 in. long leaflets and a terminal one. The inflorescence of long spiciform erect racemes, bearing numerous shortly pedicelled small reddish purple flowers.

8. PHYSOSTIGMA VENENOSUM Balf. Calabar Bean. A large leguminous climber, a native of Old Calabar, but introduced into Brazil and India. The seeds contain the well-known alkaloid Physostigmine or Eserine, very poisonous.

9. CONIUM MACULATUM L. (Umbelliferae). Hemlock. This herb has a wide distribution throughout Europe to temperate Asia and North Africa and has been introduced into both North and South America.

The species harbours several alkaloids. In poisonous doses the mind remains unaffected to the last, the classical instance of this being the death of Socrates as related so movingly by Plato in the *Phaedo*.

10. CINCHONA LEDGERIANA, C. OFFICINALIS and C. SUCCIRUBRA (Rubiaceae). Trees native to the eastern side of the Andes and introduced some 60 years ago into Java and India. They contain several alkaloids, the most important from the commercial and medical point of view being Quinine. The most important species is *C. Ledgeriana*, by far the most extensively cultivated.

11. COFFEA ARABICA and other species (Rubiaceae). A shrub or small tree native to tropical Africa, but widely cultivated in the tropics. The characteristic alkaloid obtained from the seeds is Caffeine, which occurs also in Tea, Paraguay Tea (*Ilex paraguayensis*), Kola and other species.

12. PSYCHOTRIA IPECACUANHA (Rubiaceae). A small shrub, a native of the tropical forests of Brazil, but cultivated in other parts of the tropics. It is cultivated to a small extent in India and still more in the Malay Peninsula.

Emetine, the alkaloid so useful in one form of dysentery, is contained chiefly in the root bark.

13. STRYCHNOS NUX VOMICA L. (Loganiaceae). A moderate sized tree, native to India, Ceylon, Burma, Cochin-China and parts of the Malay Archipelago.

The seeds yield several alkaloids, the chief being Strychnine. Taste is very bitter. CURARINE got from other species of Strychnos.

14. NICOTIANA TABACUM L. (Solanaceae). A coarse annual. Probably a native of Central or South America.

The leaf alkaloid is a volatile liquid, Nicotine.

15. DATURA STRAMONIUM L. (Solanaceae). A coarse weedy annual. Spread throughout the world. Daturine from the leaves and seeds. Akin to Atropine.

16. ATROPA BELLADONNA L. (Solanaceae). A large bushy herb. Central and Southern Europe, South-west Asia and North Africa.

ATROPINE from the roots and leaves. Crystalline.

17. HYOSCYAMUS NIGER L. (Solanaceae). An annual or biennial herb. Temperate Europe and Asia. Introduced into America.

Hyoscyamine from the seeds and leaves.

II. THE BIO-CHEMISTRY OF ALKALOIDS.

By T. A. Henry, D.Sc. (London).

(*Director Wellcome Chemical Research Laboratories.*)

The first clearly defined alkaloid—morphine—was isolated in 1817, so that over a century has elapsed since the interest of chemists in these products was first evoked. During that period hundreds of new alkaloids have been discovered and described, and great progress has been made in the determination of their intimate structure. The precision which has been reached in some branches of work of this kind may be gauged from the fact that last year conclusive proof of the constitution of the rare opium alkaloid, codamine, was furnished by Prof. E. Späth of Vienna by the use of only 0·2 gm. of the original specimen of this alkaloid isolated from opium by O. Hesse in 1870.

The constitutions of quinine and the more important related alkaloids derived from cinchona have been known for some years, and syntheses of this group of alkaloids cannot now be long delayed. The structure of all the commoner alkaloids of opium is known, with the exception of the most important of all, viz. morphine and its close relatives, codeine and thebaine, and here only details remain to be settled. Similar progress is being made with other alkaloids of special therapeutical interest such as emetine and strychnine, and the activity in alkaloidal research at Manchester, Oxford, Marburg and Vienna is such that one wonders how long the known supply of "alkaloids of unknown constitution" will hold out. The organic chemist can reasonably claim that he has done his part in adding to the knowledge of alkaloids, but it is of interest to note that in spite of all this activity no natural alkaloid has yet been replaced commercially by its synthetic equivalent, though this could be done in a number of cases if necessity for it arose. The fact that man is still dependent on natural sources for supplies of these indispensable medicinal products makes it all the more surprising that next to nothing is known of the part they play in the physiology of plants. This lack of knowledge is no doubt due to the facts that the most important alkaloidal plants are grown in the Tropics, where facilities for bio-chemical research are still severely restricted, and that, except in the cases of cinchona and

opium, production is scattered and on a small scale, so that there is no organisation for the systematic research necessary to secure such information. Alkaloidal plants, such as those of the Solanaceae and the Leguminoseae are however available in temperate regions, and the numerous problems presented by the distribution, origin and function of alkaloids in plants will no doubt eventually attract the attention of the bio-chemist. At present the bio-chemistry of alkaloids consists of little more than casual, unrelated observations with much, more or less, plausible speculation.

Alkaloids may be defined as naturally occurring, relatively complex, basic substances usually exhibiting marked physiological action, but the term is not always used in this strict sense outside chemical circles. It is not uncommon to find the name applied to such substances as digitoxin, strophanthin and santonin, that is, to naturally occurring, physiologically active substances, which contain no nitrogen and are not basic. That is the essential difference and, broadly speaking, alkaloids are classified for convenience of description according to the way in which the constituent nitrogen is built into the molecule. The simplest alkaloids are derivatives of open chain or aliphatic amines, whilst the more complex have as nuclei, closed heterocyclic chains in which the nitrogen is the heterogeneous element. The more complex alkaloids are further subdivided, according to the nature of these heterocyclic rings into derivatives of pyrrolidine, piperidine, glyoxaline, etc., and still further according to the nature of the proximate structure of which the primary heterocyclic ring forms part, into tropane, granatane, quinuclidine, quinoline, isoquinoline, indole, purine etc., derivatives. Such schemes of classification become increasingly difficult as knowledge of the structure of alkaloids grows and though they are always misleading something of the kind is necessary for purposes of general discussion.

Taking a group of plant species so closely related as to be included in one natural order, it is reasonable to assume that the plants concerned will possess a common metabolism and have most of their characteristic constituents in common. That seems to be true as regards alkaloids in only one natural order, viz. Amaryllidaceae in which the characteristic alkaloid is an *iso*quinoline derivative, lycorine or narcissine which has been found in at least ten genera of the order. It is also true of such a characteristically alkaloidal order as the Papaveraceae where in spite of the many different alkaloids that may be present in a single plant—there are at least 25 in the opium poppy—all are *iso*quinoline derivatives, so far as is known, and all can be regarded as arising by a common process.

A more usual state of things is presented by such orders as the Solanaceae and the Leguminoseae. In the former three well-defined and distinct groups of alkaloids occur, typified by hyoscyamine (tropane nucleus), nicotine (piperidylpyrrolidine nucleus) and solanine (a complex alkaloidal glucoside of unknown constitution) respectively. Hyoscyamine occurs in several genera, Datura, Atropa, Scopolia, Duboisia and Hyoscyamus, nicotine in one only, Nicotiana, whilst the solanines are found only in Solanum species.

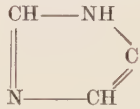
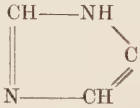
Much the same state of things is found in the Leguminoseae where cytisine (quinoline condensed with pyrazine or pyrazole as a nucleus) is the most widely distributed alkaloid having been found in *Anagyris*, *Baptisia*, *Cytisus Laburnum*, *Euchresta*, *Genista*, *Sophora* and *Ulex*. The alkaloid sparteine, which is a quinuclidine derivative, a characteristic which it shares with the principal cinchona alkaloids, is found in the genus Lupinus and in one species of *Cytisus* (*C. scoparius*). Trigonelline,

a simple pyridine derivative, is found in *Trigonella* and in *Pisum*. Hypaphorine and eserine, respectively simple and complex derivatives of indole occur in *Erythrina hypaphorus* and *Physostigma Venenosum*. Finally vicine, probably a purine glucoside, occurs in *Vicia* spp. and there are less well-defined alkaloids in other genera of the order. In view of this variation in the type of alkaloid, which may occur within a single natural order or even within a genus, as in *Cytisus*, it seems clear that by whatever process alkaloids may be formed in plants, it must be a process which from similar materials must be capable of giving rise to a variety of products.

None of the alkaloids so far mentioned are to be found in plants of more than one natural order, but berberine, one of the best known of the *iso*quinoline alkaloids, has been recorded in at least 14 genera belonging to five natural orders, Ranunculaceae, Berberidaceae, Menispermaceae, Papaveraceae and Rutaceae.

It is common ground with authors, who have put forward suggestions as to the mode of origin of alkaloids in plants that the primary materials must be amino-acids, produced by the breaking down of proteins, but it is at least equally probable that they are formed as by-products in the building up of proteins. The former process can be demonstrated, so far as the production of simple bases—too simple to be regarded as alkaloids—is concerned from what is known regarding the hydrolytic products of gliadin, one of the proteins found in rye and the amino-acids and amines found in ergot of rye and presumably produced by the action of this fungus on the proteins of rye grain. As shown in the following table, the six amino-acids from leucine to lysine are all found among the hydrolytic products of the gliadin of rye, whilst in the fungus the same animo-acids are represented by the corresponding amines, *iso*amylamine to cadaverine, produced in each instance by decarboxylation of the amino-acid, of which in most cases some also survives in the fungus.

Simple Bases of Ergot of Rye.

1. Leucine	$CHMe_2.CH_2.CH(NH_2).COOH$	in rye and ergot
*iso*Amylamine	$CHMe_2.CH_2.CH_2.NH_2$	in ergot
2. Aspartic acid	$COOH.CH_2.CH(NH_2).COOH$	in rye and ergot
3. Histidine		in rye and ergot
Ergamine		in ergot
4. Tyrosine	$HO.C_6H_4.CH_2.CH(NH_2).COOH$	in rye and ergot
Tyramine	$HO.C_6H_4.CH_2.CH_2.NH_2$	in ergot
5. Arginine	$NH_2.C(NH).NH.CH_2.CH_2.CH_2.CH(NH_2)COOH$	in rye
Agmatine	$NH_2.C(NH).NH.CH_2.CH_2.CH_2.CH_2.NH_2$	in ergot
Putrescine	$NH_2.CH_2.CH_2.CH_2.CH_2.NH_2$	in ergot
6. Lysine	$NH_2.CH_2.CH_2.CH_2.CH_2.CH(NH_2).COOH$	in rye
Cadaverine	$NH_2.CH_2.CH_2.CH_2.CH_2.CH_2.NH_2$	in ergot

This sort of process gives us no clue to the origin of the real alkaloids, ergotoxine and ergotamine, found in the fungus and to which there is nothing analogous among the constituents of rye grain or their hydrolytic products.

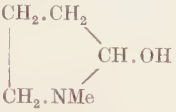
Of all the suggestions that have from time to time been put forward to account for the formation of alkaloids the most useful is that published by Robinson in 1917. These views have the great advantage that they postulate the pre-existence in the plant of nothing not known to occur there, or at any rate not likely to be present, they assume only the possibility of reactions, which there is every reason to believe do occur in plants, and Robinson has himself shown by the synthesis of tropinone and pseudo-pelletierine in the laboratory by these processes, that the latter can take place at atmospheric temperature.

On the basis of these views the following explantion of the formation of hygrine, the simplest alkaloid found in coca leaves is given.

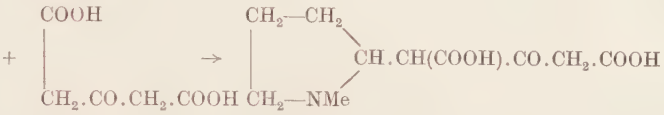
Stage I. Oxidation and methylation of ornithine by formaldehyde to a carbinolamine of the pyrrolidine series.

$$NH_2.CH_2.CH_2.CH_2.CH(NH_2).COOH + H.CHO \rightarrow$$

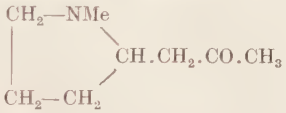
$$NH_3 + CO_2 + NHMe.CH_2.CH_2.CH_2.CHO \rightarrow$$



Stage II. Condensation of the carbinolamine with acetonedicarboxylic acid.



Stage III. Decarboxylation of the condensation product to (in this case) hygrine.



By a similar condensation of two molecules of the carbinolamine with one molecule of acetonedicarboxylic acid, a base isomeric with cuskhygrine would be produced, whilst, if Stage I is carried a step further, ornithine might yield succindialdehyde and methylamine, thus:

$$NH_2.CH_2.CH_2.CH_2.CH(NH_2).COOH + 2H.CHO \rightarrow$$
$$2NH_2.CH_3 + CO_2 + CHO.CH_2.CH_2.CHO$$

and from these two substances and acetonedicarboxylic acid, Robinson has shown that tropinone can be produced in the laboratory, and tropinone is a probable intermediate in the production of tropine and eventually of hyoscyamine in the plant.

Still keeping to the same materials, ornithine and acetonedicarboxylic acid, it is possible to represent by reasonable variations in the same processes the formation of nicotine, thus affording an explanation of the apparent anomaly referred to above that plants so closely related as to be placed in the same natural order Solanaceae may produce what at first sight appear to be totally different types of alkaloids, viz. hyoscyamine and nicotine.

There has thus been produced on the chemical side a promising view, supported by experimental evidence, of the processes by which even the most complex alkaloids known could originate in plants, and it now remains for plant physiologists and bio-

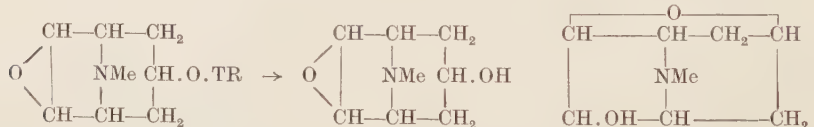
chemists to take up the subject from the biological side and prove or disprove the validity of Robinson's suggestions.

There is one other problem in connection with the bio-chemistry of the alkaloids, which must be referred to. The importance of alkaloids to man is obvious but their value to the plants which produce them is not so clear. Three views have been held as to their function in plants:

(*a*) that they are produced as protective agents,
(*b*) that they are plastic products destined for further use by the plant,
(*c*) that they are merely accidental products of metabolism, that is, waste products.

The first view has all the appearance of having been put forward without serious consideration. If toxic constituents protect plants, animals must be aware that such plants are dangerous and avoid them. There is however no evidence that this happens. Scarcely a year passes in which cattle are not poisoned in England by eating branches of the yew tree, and in countries like Australia, South Africa, and New Zealand where toxic plants have not been largely eliminated from the pastures by generations of careful farming, as they have in England, such plants cause serious annual losses to the pastoralist.

No experimental evidence of great value has been put forward for the view that alkaloids serve as plastic products, in the sense that they are used up by the plant liberating stored energy and being reduced to simple degradation products, but the sounder part of this view, suggested by Bayliss, that alkaloids may serve as stimulants of some kind has never been tested experimentally. It has been applied, with more reason perhaps, by Armstrong to certain of the glucosides, and it should not be overlooked that more alkaloids may occur in plants in the form of glucosides than is at present suspected. At first sight the fact that alkaloids are relatively stable and not highly reactive substances under the conditions obtaining in plants, whereas those glucosides which Armstrong regards as means of storing stimulants, produce on hydrolysis highly reactive substances, discounts the view that alkaloids can fulfil such a function, but it is interesting in this connection to remember that Willstätter has shown recently that the alkaloid hyoscine when hydrolysed by the pancreatic lipase yields the labile substance, scopine, which very readily passes into the stable substance oscine long familiar as the hydrolytic product of hyoscine, when the hydrolysis is brought about by acids or alkalis.



Hyoscine (TR = Tropoyl radical) Scopine Oscine

However that may be, the bulk of alkaloid found in any particular plant appears normally to behave as would be expected of a product formed accidentally and without ulterior purpose. It is typical of reactions with organic materials, whether produced by chemical or biological agency, that they are rarely complete or proceed wholly in one direction, and it is to be expected that in the synthesis of proteins from simple amino-acids some by-products will be formed, and that in the degradation of proteins reactions will occur between the amino-acids produced and other substances present in the plant at the same time. When metabolism is active the quantity of

these by-products formed is certain to increase just as the dump-heaps of a blast furnace grow with increased output of metal. It is often carelessly argued that alkaloids, tannins and other normal secondary constituents of plants must be plastic products because their amount is greatest when metabolism is most active but the fact is that real plastic products should be difficult to find when metabolism is most active, because they must be constantly used up and it is only when metabolism slackens that they should begin to accumulate. Perhaps the most convincing piece of work so far accomplished bearing on the function of alkaloids in plants was published by Dr H. E. Annett in India in 1921. He showed quite clearly that in the opium poppy, where the alkaloid-yielding latex is found in the walls of the unripe capsule, that neither the application of nitrogenous manures nor any change in environment affected the proportion of morphine found in the latex, though the quantity of latex formed might be so influenced. In a well-regulated factory one would expect the proportion of waste product to remain constant and the total quantity to increase or diminish as the environment was favourable or unfavourable to factory operations.

Annett also found that in lancing capsules for opium the whole of the morphine was removed in the first few lancings, later lancings yielding latex free from morphine. Further, the seed produced from lanced capsules was as good in quality as that formed from unlanced capsules, so that the latex does not appear to fulfil any special function in connection with the seed during the ripening of the capsule. In addition to special evidence of this kind, the general conditions under which alkaloids are produced and stored in plants, support the view that they are waste products.

Alkaloids are not as a rule found in quantity in seats of active metabolism, such as the leaves, except in short-lived plants where other means of storage are not readily available and even in these cases they are eventually transported to the rinds of the fruits as in the opium poppy, to the coats of the seeds as in some of the solanaceous plants or to the roots as in biennial plants. In perennial plants the usual source of alkaloids is the bark or the seeds, and in the latter, for example in Strychnos, strychnine and brucine are found mainly in the seed coats, which are thrown off and the alkaloids lost when the seed germinates.

III. THE MEDICAL ASPECTS OF THE ALKALOIDS.

By J. W. Trevan.

(*The Wellcome Physiological Research Laboratories, Beckenham, Kent.*)

The number of alkaloids which are used in medicine is small compared with the number known. Out of some 800 alkaloids described in Henry's *Plant Alkaloids* only comparatively few have a certain place in therapeutics. There have been, of course, claims that a very large number of extracts containing alkaloids have valuable therapeutic effects, but the number of alkaloids for which there is both scientific evidence from the laboratory, and a consensus of reasonable clinical opinion that they are valuable is about 27. There are many preparations which the increase of therapeutic scepticism in the latter part of the nineteenth century swept out of use, but I think the alkaloids enumerated below probably will be retained in scientific medicine for some time to come. Two indeed have only recently been introduced into general use—sparteine and ephedrine—and I think it is likely that new alkaloids or new uses

for old alkaloids will increase the list still further. The scientific evaluation of the therapeutic properties of a drug on man is an operation of extreme difficulty, much more difficult than its preliminary examination in the laboratory.

Alkaloids used in medicine may be divided into two groups, one producing specific effects on parasites infesting the body, the other producing physiological changes in the body which counteract the disturbances of function set up by disease of rendering possible certain therapeutic procedures involving interference with body functions. In the first group are the drugs given in Table I.

Table I.

Alkaloids having an antiparasitic action.

Alkaloid	Use
Quinine group	Destruction of malarial parasites
Emetine	Destruction of *Amoeba histolytica* (dysentery)
Conessine	Destruction of *Amoeba histolytica* (dysentery)
Pelletierine	Anthelminthic
Arecoline	Anthelminthic.

There are a few other alkaloids to which antiparasitic properties have been attributed but the evidence is not conclusive.

The alkaloids of the second group can be subdivided according to their site of action.

(1) Drugs used for their Action on the Central Nervous System.

A. *Depressants.*

1. *Morphine* is the oldest member of this group. It produces its principal effect in the body by diminishing the activity of the cerebrum. It is probably still the most valuable drug for this purpose. Nothing approaching the effect of morphine is produced by any of the modern synthetic hypnotics which pour out in a vast spate year by year from Continental chemical laboratories. The sleep produced by morphine is a nearer approach to natural sleep than any other drug produces. After taking the ordinary hypnotic the patient generally awakes with a headache comparable to that "morning after the night before" sensation which succeeds the sleep produced by over-indulgence in alcohol—which of course is the physiological type of the synthetic hypnotics. This unpleasant effect is absent after morphine and probably because of this very fact morphine is more prone to give rise to the drug habit. I feel that it is illogical to suppose that by any synthesis a drug will be produced equivalent to morphine in therapeutic effect but not prone to give rise to the drug habit. After all the foundation of the drug habit must really depend on the efficacy of the physiological effect produced. The morphinomaniac started his habit because of the therapeutic effect of the drug. Morphine also has a special action where sleeplessness is produced by pain. Much larger doses of the synthetic hypnotics have to be given where there is any great pain. This suggests that morphine has a special action on the ganglia in the base of the cerebrum which are specially concerned with the reception of sensory impulses, and indeed there is evidence from the reaction of the cat that the highest centres in the cerebrum are stimulated by morphine in small doses. Pain at any rate disappears before consciousness is affected when morphine is

administered, whereas the highest part of the cerebrum is put out of action first by hypnotics. Morphine and its derivative heroin are also valuable for their power of diminishing cough by depressing reflex excitability.

2. *Hyoscine* is also used for its depressant effect on the cerebrum. It is used in acute mania. Morphine is not much good in this connection—which is evidence in favour of the suggestion outlined in the last paragraph as to the action of morphine on the cerebrum. Hyoscine has the disadvantage of having certain peripheral effects on the pupil and the secretory glands similar to that of atropine. The peripheral action of atropine is due almost entirely to the laevo-hyoscyamine which it contains. The optical isomer dextro-hyoscyamine, the other constituent of atropine, has no such peripheral action and we are trying it at the moment as a substitute for hyoscine, but the results are not complete.

B. *Stimulants.*

The most important alkaloid used for stimulating the central nervous system generally is *strychnine*, which acts on all parts of the central nervous system, increasing the rapidity with which the organism responds to sensory stimuli and diminishing the latent period of reaction. It is almost confined to uses as a general tonic.

One alkaloid has recently found a place in therapeutics because of its more or less selective activity on the part of the central nervous system which is responsible for the regulation of respiration, namely *lobeline*, which stimulates respiration in a very striking fashion.

Apomorphine stimulates the vomiting centre.

Caffeine also has a stimulating effect on the cerebrum. I have seen acute mania develop as a result of caffeine poisoning, and we all know its effect in the form of tea.

(2) Drugs Acting on the Peripheral Nervous System.

A. *On the involuntary nervous system.*

The alimentary tract, the vascular system, the secreting glands, the sweat glands, the muscle of the eye and various other structures are under the control of two sets of nerve fibres which in general have opposing effects on these structures. One set of these fibres goes by the name of the *sympathetic system*, and the other by the name of the *autonomic nerve system.*

(*a*) *Drugs acting on the sympathetic system.*

Stimulants. The body itself produces an alkaloid which is concerned with the stimulation of the sympathetic system, namely *adrenalin.* There is only one alkaloid which has found extensive application in therapeutics for its effect on the central and sympathetic nervous system, and that is *ephedrine*, which has an action very similar to that of adrenalin. Its chemical formula is somewhat similar (see Fig. 1). It acts just like adrenalin by increasing the pulse rate, increasing the extent of the contraction of the heart, raising the blood pressure by causing contraction of the smooth muscles of the walls of the arterioles and it dilates the bronchioles. It is much more stable than adrenalin because of the absence of hydroxyl in the phenyl group. Larger doses have to be used of it than of adrenalin, but it can be administered by mouth whereas adrenalin is almost without action when taken by mouth probably because it is destroyed before it is absorbed. The drug comes from a species of *Ephedra* found in China and records of its use are said to be in existence dating from 5000 years ago.

It seems likely that this drug will find great usefulness in the treatment of asthma, the immediate cause of which is a spasmodic action of the bronchioles. An adequate

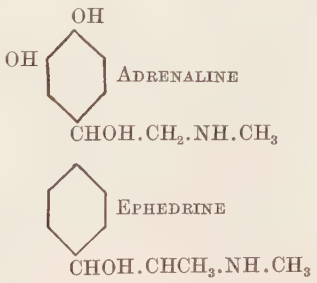


Fig. 1.

dose of ephedrine given by mouth relieves the condition in a few minutes in most cases. Other drugs which stimulate the sympathetic that are found in plants are *hordenine* and *tyramine* but they are very little used in therapeutics.

(*b*) *Drugs acting on the autonomic system.*

The belladonna group of alkaloids are most important in this connection. *Atropine* is the most important drug. It is made up as already stated of equal quantities of dextro- and laevo-hyoscyamine of which the laevo- is the most active on the autonomic system. It is used principally for dilating the pupil and paralysing the accommodation of the eye, as for instance, when the oculist wishes to examine the retina or measure the optical constants of the refractive media of the eye. It has been to some extent superseded by a synthetic product *homatropine* but its use is still necessary where prolonged action is required or for children. It is also used in relaxing the bronchioles in asthma and bronchitis by paralysing the constrictor fibres which are supplied by the autonomic system. Children are very tolerant of the drug. It has occasional uses in paralysing the nerve endings of the secretory glands and is used as a test in typhoid fever in which an injection of atropine fails to cause a rise in pulse rate as in the normal human. The autonomic fibres which supply the heart through the vagus nerves are continually in activity in the normal animal, keeping a pulse rate lower than it had otherwise been. Atropine paralyses these nerves and so increases the pulse rate. In typhoid fever normal activity of the vagus is in abeyance. The vagus nerve also supplies the intestine so that the paralytic effect of atropine makes it good for colic.

Physostigmine stimulates the autonomic nerve endings, causing contraction of the pupil and exaggeration of the movements of the bowel. Its uses in medicine are to counteract the effect of atropine after an optical examination and to stimulate a paralysed bowel to contract after surgical operations.

Pilocarpine is the other alkaloid which is used for its effect on the autonomic system. It is principally used for producing sweating in kidney disease.

B. *Drugs that act on the sensory nerve endings.*

Aconite has a reputation for producing anaesthesia when applied in the form of an ointment to the skin. It is a highly dangerous drug which is going out of use.

The most important alkaloid which acts on the sensory nerve endings is of course

cocaine. It is still the best local anaesthetic available for ophthalmic purposes and for the nose and throat. It has the advantage over all the local anaesthetics so far proposed as substitutes, of causing constriction of the pupil and constriction of small blood vessels both of which properties make it indispensable for use in ophthalmic work. The various substitutes synthesised in the laboratory are displacing it in other fields, but the eye surgeon still depends on it.

(3) Drugs Acting on Muscle.

A. *Heart muscle.*

Caffeine is used as a cardiac stimulant but not extensively.

Quinidine and *sparteine* are used for their depressant action on the heart muscle. There is a clinical condition known as auricular flutter, the principal symptom of which is a very rapid pulse rate and consequent embarrassment of the circulation. The administration of either of these drugs reduces the pulse rate abruptly to normal by an action which has been worked out in detail by Sir Thomas Lewis and his colleagues.

B. *Involuntary muscle.*

The work of Macht has shown that *papaverine* inhibits the contraction of smooth muscle. The discovery of this property has led to the use of this alkaloid in the various forms of colic which are produced by spasmodic contractions of organs containing smooth muscles.

There are a certain number of alkaloids which are used for their stimulating effect on the muscle of the uterus namely *ergotoxin* (and the closely allied *ergotamine*) which is used to produce contraction of the uterus after labour, and *hydrastine* and *cotarnine* which are used to prevent excessive menstrual haemorrhage.

The alkaloids used to stimulate the kidney to secrete are *caffeine* and *theobromine* principally, and they probably produce their effects by acting on the blood vessels.

The majority of alkaloids that are used in medicine are therefore used for their action in interfering with the normal mechanism of the body. Such a method of treatment is perhaps to be deprecated. It is rather like putting sand into a clock to regulate its time-keeping properties when the pendulum has dropped off. Unfortunately we cannot always find the missing pendulum when the body goes wrong and we have to do the best we can. It is extraordinary, and, I suppose, characteristic of living things how with a little assistance the body can get along with one or more organs permanently damaged. There is one interesting recent example of the condition in which the missing link which gives rise to disturbances of function has been prepared in a form in which it can be administered—the missing pendulum has been found. I refer to the condition of excessive menstrual haemorrhage. It is becoming fairly clear that this is due to a deficiency in a hormone which can be prepared from the ovaries of cattle. The excuse for retaining *hydrastine* in our list should therefore disappear, and the hope of the physician is that with the progress of knowledge more discoveries similar to this will render the use of alkaloids and other remedies for purely symptomatic treatment less and less necessary. With regard to the drugs in Table I the ground for their use is a much more logical one. Their action is directly on the exciting cause of a disease, and it seems possible that additions to the therapeutic armament of a physician will be members of this group rather than of the other. The discovery of new alkaloids with this type of action is of course much more

difficult than that of alkaloids in the other group. We may however take some encouragement from the fact that it is not many years since it was found that Bilharziosis, which is such a plague in Egypt, can be effectively treated by this drug. With the characteristic exasperation of therapeutic research, another specific for this disease, namely tartar-emetic, was discovered almost at the same time.

IV. GENERAL DISCUSSION.

CHAIRMAN: One of the questions raised by Dr Henry was the reason for these alkaloids in plants, and he mentioned the suggestion, though I do not think he proved it, that they might be protective. Plants run great risk from insects, and I think it can be said with certainty that the presence of alkaloids is no protection. I remember how greatly the seed and seed capsules of a poppy in Ceylon were attacked by a butterfly which ate them, and in this country the Hemlock has a moth that eats inside it. There is not much evidence that alkaloids are a protection.

One question I would like to ask is whether you (Dr Henry) think there is any prospect of replacing the plant as a maker of alkaloid. In my business, as an Economic Entomologist, we are very dependent on nicotine as an insecticide, but getting it from the tobacco plant is expensive, and if we could have nicotine replaced commercially, we think perhaps it would make a difference.

Dr PETHYBRIDGE: I should like to know if it holds good in most cases that manuring has no effect on the quantity of alkaloid developed. I remember trying to grow tobacco in Ireland, which could be smoked, and in our first efforts the proportion of nicotine was about something like 14 per cent., and the smoking of it was perfectly vile. We were told that the reason was that it had had too much nitrogenous manure, and certainly the fact was proved.

Mr HOWES: I should like to ask Dr Trevan why it is that any native races who make use of arrow poisons can eat the fish without fear of consequences; they use poisoned arrows for game and eat the flesh. Surely these things have alkaloids in them. Is it merely distributed all over the animal and dispersed in small quantities?

CHAIRMAN: One of the things which attracts one about all the alkaloids is how extraordinarily specific they are in their action. In the use of alkaloids as insecticides, it is found that one will be extraordinarily toxic, and a closely related one will have no action whatever. I assume that nicotine is present as nicotine in growing leaves of the tobacco plant, but in spite of that there are a large number of caterpillars which will live and flourish on these leaves, whereas if one gets the nicotine out and puts it on the outside, the caterpillar will eat it and die. It may be that the nicotine is not present in the plant but is produced by fermentation?

Dr HENRY: With regard to the synthesis of alkaloids, it is very unsatisfactory for a chemist to have to confess that although we have been at work on these things for a long time, there is not, at the present time, any case in which a natural alkaloid has been replaced commercially by its synthetic equivalent. The nearest approach is cocaine, which has been developed by Robinson's process, and sparteine has been put on the market, which is not a very good substitute. In the special case of nicotine, I do not think very much attention has been given to that, but it is a more promising

case. I think it should be possible to produce something, but what is proved is, that a good deal of work is needed. I think it is quite likely that if quinine were synthesised to-morrow we should be unable to put it on the market in competition with cinchona.

With regard to manuring, the only effect of manuring is to increase the yield of plants and to increase the amount of alkaloid in that way, but the quantity of alkaloid in a plant is not raised. The case in Ireland was not understood and has never been explained. It merely emphasises the necessity of more work being done on that side.

As to the form in which nicotine exists, what the Chairman suggests is quite likely. The method by which alkaloids are got out of the plant might destroy glucosides, and you could have it in some form which would not be toxic, but that is a point which wants investigating.

Dr Trevan: Both questions are difficult. As regards poisons—take for instance the arrow poison—the most important types are poisons which contain glucosides of a digitarious type. To begin with, the amount they get is very small, and though enough to kill the animal is nothing like enough to kill a man. You can kill a rabbit with less than a therapeutic dose. That is one way in which I think the native who uses arrow poison escapes. The other is that by the method of injection of poison under the skin the dose to kill an animal is considerably less than that taken by mouth. Another suggestion that has been raised, though I do not think there is any good evidence for it, has been advanced in the case of fish poison; it is said that the toxin accumulates in the brain and natives are very careful not to use the cerebrum (?).

As regards the specificity of alkaloids, that is a long question, and all I know is that it is a most amazing thing that two substances quite similar in structure put into an animal produce different results, whilst two unrelated substances may have quite similar physiological actions.

JOINT DISCUSSION ON THE CONTROL OF PLANT DISEASES

Opening Addresses in the joint discussion between Sections 'K' (Botany) and 'M' (Agriculture) on "The Control of Plant Diseases" held in the rooms of Section K at the meeting of the British Association for the Advancement of Science, Leeds, September 2nd, 1927. In the chair Professor F. E. Fritsch, President of Section K.

I. Opening Speaker for Botany—Mrs N. L. Alcock, F.L.S., *Plant Pathologist to the Board of Agriculture for Scotland, Edinburgh.*

II. Opening Speaker for Agriculture—Dr William B. Brierley, F.L.S., *Head of the Department of Mycology in the Rothamsted Experimental Station, Harpenden, Herts.*

I. Botany.

A. Author's Abstract.

(1) *A short review of past measures in the control of Plant Diseases in Great Britain and how far successful.*

The rise of American gooseberry mildew. Prof. Salmon's warning against American gooseberry mildew and wart disease. Prof. Somerville and white pine blister rust. The saving of the situation as regards wart disease by the discovery of the immune varieties. Action that succeeded—methods that have not succeeded.

(2) *The present point of view and present administration of control. The essential factors for success in control are:*

(*a*) The convinced and willing co-operation of growers. This implies their share in framing legislation.

To attain this end clearness in exposition and ability to see the point of view of the grower and realisation of the business value of all control measures must go hand in hand with scientific efficiency in administration.

(*b*) Accurate scientific knowledge on the part of those administering control.

(*c*) Moderation in policy when framing rules and regulations for ordinary occasions, and brevity and conciseness in all exposition of such rules.

(*d*) Drastic measures for extraordinary occasions.

(3) *Some questions for the future.*

Plant disease control in *Agriculture.*

Margin of profit here small. Methods must be (*a*) certain, (*b*) easy, (*c*) cheap.

Examples—Bunt and Formalin.

Seed-borne Diseases.

Some 70 common diseases carried on seeds. Research needed on treatment.

Horticulture.

Plant disease control more promising in horticulture. Margin of profit higher. More labour available. Plant sanitation essential. Prevention better than cure.

Forestry.

Prevention of disease in nurseries and inspection and control of importation.

B. *Opening Address.*

THE CONTROL OF PLANT DISEASES.

By N. L. Alcock, F.L.S.

(*Plant Pathologist to the Board of Agriculture for Scotland.*)

"Be ye ashamed oh ye husbandmen; howl oh ye vinedressers, for the wheat and for the barley: because the harvest of the field is perished. I have smitten you with blasting and mildew."

Joel i. 11 and Amos iv. 9.

The idea that disease of men, of cattle and of plants was a direct act of punishment from the Deity has gradually waned. The view that diseases of men were preventible came first. Veterinary Science has slowly developed and is beginning to have the recognition that is its due, and the youngest scion of medicine, Plant Pathology, is now standing on unsteady feet looking out at a rather unfriendly and sceptical world. Folk still waver between hanging small pieces of looking-glass over the potatoes at the new moon and spraying with Bordeaux Mixture. Ignorance of the nature of plant disease is exemplified by the letter, among the files of the Ministry, saying the writer knew Wart Disease of potatoes was infectious because it had come out all over the baby! But the ignorance of the otherwise highly educated on the subject of plant disease is more troublesome and possibly more profound than that of the peasant.

Continual steady losses go on and it is only by a series of serious attacks that any conviction of their importance is brought home. The first real recognition of plant disease came with the American Gooseberry Mildew. There have always been far-seeing men who saw the importance of disease. Prof. Salmon of Wye in 1905, while the Gooseberry Mildew was still no further than Ireland, gave a clear warning of the necessity for the legislative control of both American Gooseberry Mildew and the potato Wart Disease. Another striking warning, given when the importance of plant disease was not so generally recognised, was that of Prof. Somerville in 1909 (*Quarterly Journal of Forestry*, III, 233). He says, speaking of *Cronartium ribicola*, white pine blister rust, "the disease...is said to be absolutely unknown in America....But it is to be feared that the day is not far distant when it will gain a footing in North America, and if it spreads there, as it has done in Europe, the loss that will result can only be described as appalling." I believe the loss to-day is reckoned at millions of pounds.

But neither the gooseberry disease, which after all attacked a non-essential food, nor the white pine blister rust whose ravages occurred beyond the Atlantic, really awoke England. The first real awakening came with Wart Disease, which though described as a new disease of the potato in England by Prof. Potter and by Mr Massee, in 1902, was not recognised as a danger till some years later.

These two diseases brought legislation. The gooseberry mildew legislation was a feeling in the dark, a stumbling after rules that should help, and it did not always attain the end sought. Gradually experience taught the necessary restraint and moderation, and the amended legislation met the requirement and also the disease for some reason lessened gradually. Let us say because of the legislation, but probably an ebb and flow as yet not understood, occurs in all these troubles, as in human infectious diseases.

Prof. Salmon again spoke in warning of the trouble Wart Disease would bring, but little was heard of Wart Disease for a few years and no very drastic measures were taken. But the disease spread and the American Gooseberry Mildew flourished, and in 1907, another landmark in control appeared with the Destructive Insects and Diseases Act of 1907, an enlargement of that of 1877, which dealt with the Colorado beetle. This was really the initial stage of legislation for Plant Disease Control and brought the whole subject into prominence. The institution of Inspectors to administer the control and Mycologists and Entomologists to recognise and teach others to recognise the pests, was bound to follow and did so.

A third landmark emerged in 1909. This was the discovery that certain varieties of potatoes were immune to Wart Disease. The work resulting in this discovery was carried on over a number of years, and with it the names of Mr Gough and Mr Snell will always be associated. No one knows yet why certain potatoes are immune to this disease, but this fact has stood out for the last 15 years in the annals of Plant Disease Control. So far the immunity has not broken down to any great extent. There are hints in some of Mr Anderson's new work of the possibility of so virulent an infection that this immunity may break down. But we can still say, to quote Dr Pethybridge's short and cogent speech on control, "Thank God for the immune varieties." The Geneticists have helped much, once the discovery was made. Immunity appears to be a Mendelian character and therefore breeders can breed towards immunity with some chance of success, although every new variety has to be carefully tested. Plants that do not take disease are, of course, the ideal and there is plenty of work for the Geneticist in producing plants of all kinds that produce acceptable fruit abundantly, mature quickly, are hardy and resist disease. Till that Millennium we must continue to try to control disease and the value of our attempts to control disease will depend on the simplicity and possibility of the methods we put forward and the clearness with which the knowledge is placed before the grower.

The Phytopathological Service in England.

The service consists of two main sections:

A. *The Control or Official Section.* This consists of:

(*a*) the *Pathological staff* at the Pathological Laboratory of the Ministry of Agriculture.

Entomologist (Mr Fryer). *Mycologist* (Dr Pethybridge). Assistant Entomologist and Assistant in Entomology. Three assistants in Mycology.

(*b*) An administrative unit forming part of the *Horticulture Division* in Ministry of Agriculture, Whitehall, *i.e.* that part of the Horticulture Branch administering the Destructive Insects and Pests Acts.

(*c*) *The Ministry's Inspectorate*, about 30 of whom have special qualifications in regard to Plant Pests and Diseases, though not entirely employed on this work. (All have been specially trained in a short course at the Pathological Laboratory.)

B. *The Advisory and Research Sections.*

(*a*) *The Corps of Advisers*, consisting of an entomologist and a mycologist in each agricultural province. Fourteen in number, *i.*e. 28 advisers.

(*b*) *The Research Workers* (about 20 or more) in both Entomology and Mycology. These are at Rothamsted Experimental Station, and also attached to Long Ashton Fruit Station, Bristol, The Imperial College of Science, London, The Fruit Station at East Malling, Lee Valley Station, Cheshunt and the London School of Tropical Medicine (Eelworm work) and elsewhere.

So much for the personnel—the essential factors for success in the control of plant disease are several, but the most important one of all is the convinced and willing co-operation of the grower. This implies his share in framing legislation, his representation in some form of advisory council. Unless the grower really works hand in hand with the Government official, no effective step can be taken. In many cases, the fault lies rather with the scientist than with the grower. The man who is making a living at a very intricate and difficult profession, who has probably been many years at it and often follows his father before him, is usually a shrewd and capable man. In Scotland the level of intelligence and education among the growers is higher than in England. His interest in a new way of fighting disease can always be aroused. But the effective action to follow this stimulus must be founded on sane principles. The business value of the control measure must never be forgotten. The value of the labour, at the time that it is suggested it should be employed, must always be taken into consideration. The value of the materials and use of machinery may exceed the narrow margin of profit in agricultural operations. The cost of the remedy must not exceed the value of the crop. The grower will work with us if we give him the chance. Never tell him to do anything that, in all probability, he will not do, that is too difficult, too complicated, too troublesome. Laws that are not carried out bring the law into disrepute and teach disregard of the law.

Secondly, the knowledge on the part of those administering control must be accurate and wide and above all practical. For instance, in some parts of Scotland spraying gooseberries for American Gooseberry Mildew with plain washing soda is cheap and effective. In other parts of Scotland this spray will burn the bushes badly and destroy the hope of a crop. If you advise a control measure that does harm you may wait long for the trust of the grower to return.

Thirdly, as to details of method. Familiar measures should be used. A tablespoon = $\frac{1}{2}$ oz., 20 oz. = 1 pint. For instance, the common 2-oz. tobacco tin will hold 4 oz. of liquid. Therefore a 2-oz. tobacco tin three-quarters full will, when poured into a gallon of water make a 2 per cent. solution, and both gallons and

2-oz. tobacco tins are well known. Both cubic centimetres and percentages should be avoided. In all control, common sense must continually be used.

Clearness in exposition is most essential. Not every practical scientist has the gift of making the facts found out by research clear so that "he who runs may read." But obviously this must be done and rules, orders, leaflets should all be in plain, simple English. As to our leaflets, I have often thought that for those for whom they were meant, a leaflet of one page with a good picture, and a good naked eye description, and the best single method of control is the ideal.

Moderation in policy when framing rules and regulations for ordinary occasions, and again absolute clearness in exposition of such rules, is necessary.

But, now and again, on the extraordinary occasion, the most drastic measure will be the wisest. When a disease appears for the first time in a country and has not spread beyond one or two fields and gardens, could all the contents of the garden, all the crop of that field be put on a bonfire much might be saved. Total destruction of all the disease and all possibly infected material is needed.

Seed-Borne Diseases.

A question that should be investigated and is likely to be discussed more in the near future, is that of the common seed-borne diseases. Many seeds carry loose spores on them (*e.g.* wheat-bearing bunt spores); many have a resting mycelium (*e.g.* flax seed with *Colletotrichum linicolum*) and many bear the fructifications of a fungus disease (*e.g.* sugar-beet seed carries both *Phoma betae* pycnidia and the sori of the rust *Uromyces betae*). *Phoma betae* produces black leg, an exceedingly troublesome disease of seedling beet. There are at least 70 common diseases carried on seed.

Research is needed, especially to find more easy and efficient methods of dealing with these diseases, such as the formalin method for bunt and the hydrogen peroxide method for celery seed and celery leaf spot.

Plant Disease Control in Agriculture.

We have not been faced by the appalling epidemics of some lands. "Fortunately or unfortunately Great Britain has never had a disastrous plant disease epidemic," says Dr Boyce. In the last ten years America says they have lost £100,000,000 through *Puccinia graminis* on wheat alone. But the constant steady toll taken in Great Britain is not noticed, and each year amounts to a very large total. We lose by preventible plant disease, tens of thousands of pounds.

In agriculture the margin of profit is small, the labour scanty.

Methods of control in agriculture must be (*a*) certain, (*b*) easy, (*c*) cheap, (*d*) safe. A good example is the formalin method of treating bunt. A bad example of a method that is neither easy nor safe is any of the dusting processes, where the dust is poisonous and the operator advised to wear a gas mask.

But the greater field for control in Plant Disease lies in Horticulture. The margin of profit is higher, more labour is available, more good can be done. There is no lack of interest on the part of the fruit grower, at any rate on the part of the good English grower and all the Scottish growers! He is more anxious that his diseases should be overcome than any scientist can be for him. The question of preventive medicine is apt to be overlooked. It is much better to avoid disease than to overcome it. Plant sanitation, good clean cultivation, destruction of all diseased plants, and parts of

diseased plants, and indeed constant destruction of all dead branches, clippings, rubbish and refuse by fire, even the extirpation of weeds, are all methods of plant disease control.

The selection of site is very important. Larch in a low damp site will suffer from larch canker and the incidence of canker on apple trees will lessen as an orchard climbs up a slope. Sour soil will increase club-root.

A great advantage is gained by working with a Botanic Garden. Every Plant Pathologist should really be an expert gardener. As this is not possible, he should work within reach of the expert gardener. Of all diseases that plants suffer from, a great many are not mycological at all. The knowledge of plants, their life and their ways that the really experienced gardener has, is more valuable than can be expressed. At Kew, Mr Coutts, the Assistant Curator, used to say he was the fifth member of the Pathological Staff—every Pathological Staff needs such a fifth member.

The Pathological and cultural knowledge available at the Royal Botanic Gardens, either Kew or Edinburgh, will keep the scientist from being lop-sided.

Both for Horticulture and for Forestry, the great importance of nurseries should be recognised. In Horticulture we can continue to look after our orchard or garden throughout the development of the plant, but in forestry the nursery is usually the one opportunity when disease can be eliminated. To be eliminated, it must be recognised—and never sent about from one nursery to another. In Horticulture and in Forestry much has been suffered in the past by diseased plants being brought into the country. Two motives, one good and one bad, are usually responsible. Good, interesting and useful plants are brought from distant countries. Our gardens have been wonderfully enriched by the Chinese plants of recent years and when these importations have been done through a Botanic Garden, little risk is run. The other motive is the passion for cheapness, the hope of a bargain—some of the very cheap importations are not good. They are not new but only cheap. The classic instance of this trouble is the introduction into America of cheap young white pines and the millions of pounds loss that followed the white pine blister rust that came with them.

To avoid disease is better than to control it.

II. Agriculture.

A. *Author's Abstract.*

(1) *Scope of Discussion.*

(2) *Research Aspects.*

(A) *Centres of Research.*

(i) Source, training and supply of men. Financing and staffing of laboratory, field and administrative services.

(ii) Types of research centres. Gradation from pure to applied work. Universities, research foundations, crop stations, government and extension services, commercial services. Source of monies and type of centre in relation to scope of work, integration and administrative control.

(B) *Fields of Research.*

(i) Principles of control. Disease surveys; plant hygiene and sanitation; plant protection; escapement of disease; exclusion of disease. Effectiveness of methods in relation to expense, social, economic and political implications.

(ii) Some primary general issues.

(3) *Applied Aspects.*

(A) *Popularisation of Knowledge.*
Oral instruction, field service, printed matter. Relative values of the several avenues.

(B) *Application of Knowledge.*
Liaison mechanisms; official, commercial, institute and extension, *ad hoc*, personal.
Comparative values of the several mechanisms in relation to types of knowledge and practice. Suggestions regarding organisation.

(4) *Essential problem for discussion is the integration of practice and research.*

B. *Opening Address.*

THE CONTROL OF PLANT DISEASES.

By William B. Brierley, D.Sc., F.L.S.
(*Head of the Department of Mycology, Rothamsted Experimental Station, Harpenden.*)

Introduction—scope of discussion.

In opening, on behalf of Section 'M,' a discussion on the "Control of Plant Diseases" I wish to keep the idea of disease in plants as wide as possible, a more inclusive concept than that suggested, perhaps, by Mrs Alcock in her address. As Section 'D' (Zoology) is not officially represented here, I presume that disturbances caused by the attack of insects and other animal parasites, usually included in the sphere of economic entomology, do not, except in so far as the host response is concerned, come within our purview. We are thus left with, on the one hand, what I may call organic troubles resulting from an excess or deficiency in one or more of the factors of the plant's physical environment—light, temperature, humidity, food supply and so forth and, on the other hand, with diseases resulting from contact with certain factors of the plant's biological environment—invasion of host tissues by vegetable parasites such as certain flowering plants, fungi, bacteria, slime-moulds and the viruses—whatever these latter may be. I take the usual American and continental European view that the term "mycology" is a misnomer for "plant pathology" and that our subject, plant diseases, covers the field I have indicated. It seems to me essential for fruitful discussion that this broad concept of plant disease should be maintained throughout.

Our subject may be approached from two sides, one, the acquirement of knowledge, or the research aspect and two, the application of knowledge or the applied aspect. In plant pathology, as in many other sciences, these two aspects are separated by a

broad chasm, that between research and practice or in the present instance between laboratory and field. We are already in possession of a great amount of knowledge which, if only it could be applied, would go far to solve many of our most urgent problems of disease. On the other hand, there are many field problems of vital importance which, as yet, have scarcely come within the field of view of research men. Further, the practical cultivator often has an invaluable and wide ranging fund of empirical knowledge; hardly perhaps knowledge in the organised and formulated sense, so much as intuitive practice and experience which, could it only be organised and formulated, would be of fundamental importance in scientific investigation and entirely re-orientate many of our points of view. The most imperative need to-day is to bridge this chasm and make available to each the knowledge and experience of the other—to integrate practice and research, the bridge being built to the centre from both sides. It is this bridge that I wish to discuss with you in this meeting. I shall consider the two aspects separately and begin first with the research aspects.

Research Aspects.

Under this heading I shall include the several phases of our subject which deal with the acquirement of knowledge concerning disease in plants. For our immediate purposes there are two main and correlated issues, on the one hand, the scientific workers ranging from the specialist in the research laboratory to the general practitioner in the field, and on the other hand, there are the actual problems of disease which require to be solved. For convenience I shall speak of these as "centres of research" and as "fields of research."

Centres of Research.

This sub-heading may be still further resolved into its "human aspects" and its "institutional aspects" and I shall consider these in this order.

Human aspects. In the past, and still largely to-day in this country, the study of plant disease has been regarded merely as a post-graduate and specialised development of scholastic botany. A student takes the usual degree courses in botany followed perhaps by a few months intensive study of the fungi and perhaps a year's "training research" on some minor fungus disease and is then turned out on the world as a fledgling plant pathologist. In the earlier simpler days of classification and description this "pure" botanical training of the plant pathologist and the subsidiary dependent status of the science were perhaps not harmful although, personally, I cannot help feeling that the outcome has been a narrower and more scholastic vision than has been desirable. With however the vast importance and wide scope of the science as, patently, it is with us to-day with its roots in botany, physics and chemistry, soil science, horticulture, forestry and general agriculture, I would ask you whether the view still commonly held by academic botanists in this country is any longer tenable. It is rather like a foster hen continuing to mother a turkey. The academic botanist may be right and plant pathology may be his very own wayward child, but the matter seems ripe for discussion. Let me put the issue in certain concrete questions.

In the first place, as a matter of recruiting, is the academic man with his "pure" botanical and inwardly directed vision as suitable for our purposes as the agricultural college man with his more general training and outwardly directed vision? The one is more usually town born and bred, with a townsman's outlook, and his academic training leaves him usually, with a townsman's attitude towards the regimented

growth of plants under commercial conditions of forestry, horticulture or agriculture. The other is more usually country born and bred, with daily experience of practical conditions, with the countryman's outlook and almost intuitive feeling for growing crops, and these things broadened, refined and formulated by his training in an agricultural college. The difference is largely one of mental attitude and outlook, and I would put it to you as a matter for discussion whether we do not need, as plant pathologists, men whose scientific vision is extrovert rather than introvert.

Again, *is* plant pathology merely a post-graduate specialisation of academic botany? The ordinary botanical student is trained by academic botanists as an academic botanist. Some months additional mycological study in a botanical laboratory or a herbarium does not make him a plant pathologist, it makes him, perhaps an embryo mycologist. A plant pathologist must have a general botanical outlook with considerable knowledge of the structure and genetics of cultivated plants and of their physiology, especially in relation to conditions of climate and soil, storage and transport. He must be intimately acquainted with the bacteria, fungi, etc., and this not so much from their academic aspects but from the standpoint of their activities in the glasshouse, field, plantation, transport waggon and storage shed, as causal agents of disease. He must have a knowledge of commercial conditions and practical processes in horticulture, forestry and agriculture and of practical hygiene and sanitation of cultivated plants in all general aspects which may bear relation to disease. He must have some acquaintance with economic entomology and helminthology and sufficient knowledge of physics and chemistry to develop prophylactic and therapeutic treatments such as spraying, dusting, fumigation and so forth. Finally, he must possess sufficient comprehension of the world situation in agriculture, horticulture and forestry, its geographic and economic implications to understand problems of plant introduction, national and international action relating to embargoes, quarantine and so forth.

I would ask you, is such a science merely a post-graduate aspect of botany for which the ordinary academic training is the all sufficient requisite, or is it better to regard it as a science of independent status, as distinct from botany as, for example, veterinary medicine is from zoology or engineering from mathematics? I do not want you to entertain the wrong idea that I think plant pathology can do without botany or that engineering can do without mathematics, for that is not the case. Botanical science is the rock on which plant pathology is founded and on which it must be developed. The question in my mind is whether the botany of our academic schools is the right kind of rock or whether it is not, in perhaps most scholastic centres, quite unsuitable. The fact of the matter is that, to-day, the plant pathologist, as a professional man analogous with the veterinarian or the medical man, has only in few cases the time and money to obtain his vocational training subsequent to a degree in botany except in the event of the development on a vastly increased scale of the system of Research and Travelling Fellowships, Bursaries, etc., adopted by the Ministry of Agriculture, the Cotton Research Association and certain other bodies. Only the research specialist in one or another aspect of plant pathology like the medical specialist can afford to spend several years gaining experience. To my mind the general practitioner in plant diseases will increasingly need to compromise and to obtain more of his vocational training as a part of his degree training—a degree in plant pathology. Adequate training for such a degree cannot, so far as I can see, be obtained within a pure academic school of botany. We need

for Biology something analogous to what the Colleges of Technology have done in Physics, Chemistry, Engineering, etc. I think the ideal would be a School of Plant Pathology intimately cooperating with Schools of Botany, of Horticulture, of Forestry and of Agriculture, or, if not an independent school, then administered perhaps from the School of Botany but with these contacts as an integral part of its existence. Plant pathology seems to me essentially an independent vocation as autonomous as the medical profession or the veterinary profession. Such a special vocation demands recognition, adequate stipends and provision for a career as obtains, for example, in veterinary or human medicine. A beginning in plant pathology has been made at home in the Agricultural Research Service of the Ministry of Agriculture and promised in the Empire by a visioned colonial agricultural research service, but commercial avenues have, as yet, hardly been thought of in this country or in many of our overseas dominions.

Many of my botanical friends will feel that I have been too drastic in what I have said concerning academic botany but I would beg them to remember that I am opening a discussion on behalf of Section 'M' (agriculture). Further, I have myself passed through the ordinary academic botanical training and may therefore be presumed to have a bias in its favour. On the other hand, my experience is much wider than that of most teachers of botany in that I have not only held posts on a University botanical staff but also on the staffs of Kew and Rothamsted. Throughout, and more especially since the war, I have had considerable experience with students and "practitioners" of botany, of horticulture and of agriculture both at home and abroad and the views I have put forward largely do represent the outcome of this, perhaps unusually wide experience. Certain ideas and points of view in botany have almost acquired the sanctity of the thirty-nine articles and to question orthodoxy is not popular with the botanical Episcopate. It would have been very easy for me to chant "God's in his heaven—Alls right with the world!" of academic botany and plant pathology; to utter pious platitudes about the need of research and about "pure" science so spotless and unsullied, to argue that all that is needed for the perfect plant pathologist *sans peur et sans reproche* is to make quite sure that he gets a thorough grounding in academic botany and that all will then be well, and so forth and so on. These are the simple articles of orthodox faith and if one anoints oneself with vegetable oil of self-righteousness and swims with the current plaudits are assured. It is neither an easy nor a popular position to be an inside critic and to abandon the my-subject-right-or-wrong attitude, but my personal experience is leading me to think that all is not well in the state of academic botany *in its relation to plant pathology*, and that this sickness is, not improbably, one of the main roots of our trouble in the supply and training of men for the control of plant diseases. As a botanist myself I rather hope I shall be proved wrong but, in any case the question is, I think, meet for discussion, and all I ask is that it be discussed with an open mind and without relation to the vested interests of botany.

I have not lost sight of the fact that unusual men, the leaders, will do unusual work whatever their training, and I rather think that such men will most commonly arise in the "pure" sciences; or of the fact that different aspects of a plant pathological training might be stressed accordingly as the more usual student envisaged a career as a specialist in a research laboratory, as a general practitioner or "medical officer of health" in the field, as a teacher of plant pathology, as a member of a field

inspectorate or advisory service, as an administrative officer and so forth. These, however, seem to me minor issues when considering the status of plant pathology as a science or in treating in general of the research aspects of our subject.

Let me now pass to my second sub-heading the "Institutional aspects."

Institutional aspects. A general consideration of centres in which research on plant disease is carried out shows a very wide range of types of institution or organisation. To illustrate what I mean, I may perhaps use the analogy of a political assembly in, for example, Germany. On the extreme right wing are the scholastic institutions with their die-hard "pure-science" attitude, whilst on the extreme left wing are the commercial laboratories with their purely economic attitude. Ranging from one wing to the other are all the various grades of institutions or organisations containing pathological laboratories or departments. Let me instance certain examples of each main block.

Moving away from the right-wing universities in which the outlook is essentially academic and purist, one comes to many of the great research foundations in which, although "pure research" is carried out, the view-points have a more applied direction. One may instance the Rothamsted Experimental Station in this country, the Biologischen Reichanstalt für Land—und Forstwirtschaft in Berlin—Dahlem or the Institut für Pflanzenkrankheiten in Bonn-Popplesdorf; the Phytopathological Institute in Wageningen, Holland; the Pusa Research Institute in India, and in the United States of America, the Bureau of Plant Industry at Washington, the Boyce-Thompson Institute for Plant Research and the Tropical Plant Research Foundation.

Passing still more towards the left are what may be called the applied crop stations, although the word "crop" is not so applicable in certain cases as the term "cultivation-area." In this country are the experimental and research stations at Cheshunt, East Malling and Long Ashton; certain agricultural colleges such as that at Wye in Kent, the Royal Horticultural Society's laboratories at Wisley, certain branches of the Department of Scientific and Industrial Research and of certain Industrial Research Associations and so forth. The new Amani Station in Africa and the visioned chain of Empire stations might find their place here along with more special centres such as the Hawaiian Sugar Planters' Station, the rubber stations in Ceylon and the Federated Malay States, the tea stations in India and Ceylon, the famous Dutch stations in Java and Sumatra, the West Indian Cotton Station and perhaps most of the agricultural experimental stations of the United States of America.

Of still more applied outlook are many of the "research-advisory" organisations such as the agricultural advisory officer service and the Imperial Bureau of Mycology in England, or the colonial mycological service overseas; and on the left-hand of this block stand the "advisory-research" organisations such as the Inspectorates and pathological services of the various governments, the extension services of Denmark, the United States of America, etc.

Passing to the extreme left wing one comes to the commercial organisations some of which are acquiring men of established reputation and are obviously destined to play a primary part in applied research of the future. In this country may be instanced the scientific officers of the Mond corporation or, on a small scale, such firms as Mason, Munro, Abol and so on, and in America the Bayer Co., the Niagara Co., the Pont de Nemours Co., the Bowker Chemical Co., etc.

Finally, there are the several journals in all countries which give practical advice or answer enquiries concerning plant disease.

When one surveys the wide scope and entirely uncorrelated nature of these organisations, not only from country to country but even within any one country, one realises how little economy in ideas, in men, time, energy or money there is in the present manner of their existence. One cannot help feeling that there should be, to take only those within the British Empire or an even smaller area, those in this country, much greater ease and freedom of exchange of men and ideas than exists, and much greater coordination of activities. It is imperative, however, that any co-ordination must be achieved without introducing the arid and sterilising influence of red tape, of unenlightened direction or of merely administrative control. With the increasing dependence of many of these organisations on government or public monies some degree of integration of staffs and activities seems inescapable, if only in the interests of economy. It is extremely desirable that we should realise this and take steps to ensure that any coordination shall not be in the interests of economy only, but also in the interests of pathological research and application and the best utilisation of available facilities to liberate the greatest good. Freedom in research does not come from the absence of organisation but is dependent for its very being upon organisation.

Further, if some degree of coordination were brought about in existing pathological organisations it might not only liberate much energy at present locked up in unskilled administration and the almost entire absence of any methods of business economy, so patent in most scientific laboratories, but it might result in the very positive gain of greater financial and practical support for the more right-wing institutions. At present the latter are almost entirely supported on rare endowments, private subscriptions and, ever preponderantly, on public monies but with such co-ordination that the practical man is brought to realise their potentiality for good, it might be possible to tap the "trade-purse" either for particular institutions or particular researches. Many of the primary crop stations are supported almost entirely by voluntary levy by the planters or traders of acreage "cess" or produce "cess," and there would seem no reason why this basis of support should not be extended in many directions.

Again, if only a broad and constructive policy could be applied to the integration of our teaching, research and practical organisations dealing with plant disease and cognate issues, so that right and left wings moved in unison to the one common end, the influence upon both extremes would be most salutary. Many academic schools of botany, for example, seem to live in a little cloistered world of their own far from any sullying contact with practical realities; a world in which plants exist as herbarium specimens, or pickled fragments in bottles; systematically arranged in botanic gardens or ecologically arranged in salt marshes. The drilled regiments and legions of plants living and dying on farm or plantation seem to have no meaning for them although our very civilisation depends upon such "crop botany." On the other hand, the grower surrounded by square miles of rubber or cocoa, sugar cane or wheat, with disease gaining upon him day by day, is apt to be impatient with the academic scholiast. To an autonomous plant pathology all this would be of little moment for it would work out its own salvation, but to a plant pathology, which, as in this country at present, is dependent on the schools of botany, the matter is one of serious import. What I, as a plant pathologist, wish to see are the schools of botany linked in closest intimacy with agriculture, horticulture and forestry so that botanical students

realise from the beginning that a cucumber house, a potato field or a rubber plantation are just as much objects of botanical study as the marine algae or an apical meristem.

We need enthusiastic and constructive imagination to integrate our pathological organisations from right wing to left so that the wings shall spread and yet come together in flight, so that the schools of botany shall become streams of inspiration finding their source in the world's demand for healthy crops.

So far I have been discussing the human and institutional aspects of research on plant disease and I shall now turn to what may be called the "fields of research" in plant pathology.

Fields of Research.

I shall not treat this portion of my subject in any detail as it has already been considered by Mrs Alcock in her address. The discussion falls naturally into two portions, one dealing with the general principles of control and the other dealing with specific issues.

Principles of control. There may be said to be some five primary avenues in disease control.

Firstly, are disease surveys, in which record is made of the presence and incidence of domestic or foreign diseases. Such work leads to international surveys and knowledge of the geographical and climatic relationships of disease.

Secondly, are all the problems connected with plant hygiene and sanitation, including the elimination of infective centres, the relation of nutritive and other physical conditions to parasitic diseases and to non-parasitic diseases and cultural methods for reducing the incidence of disease.

Thirdly, are the questions concerned with plant protection, such as spraying, dusting, steeping, fumigation, sterilisation, and so forth in all of which the fundamental value of intimate contact of plant pathology with chemistry and physics is becoming more and more evident.

Fourthly, are the problems of disease escapement, which comprise the selection or breeding of escaping, tolerating, resisting or immune varieties, the relation of time of planting and other cultural operations to disease, the questions of rotation and suitability of crop with all their corollaries.

Lastly, are the issues of disease exclusion, questions of plant introduction, of embargoes, and quarantines and legislative action in their domestic, national and international aspects.

It will immediately be clear, if one considers these principal fields of research in relation to the centres of research already indicated, that different types of institution or organisation are better adapted to advance progress in certain fields than in others. This is largely a question of the source of financial support and the facilities and men available. Thus, problems of disease survey and disease exclusion would seem best fitted to government pathological services with their adjuncts. Problems of plant hygiene and sanitation and disease escapement would on the whole seem most suitable for study by agricultural, horticultural and forestry centres. Much work concerning plant protection might perhaps profitably be carried out by the commercial organisations and so forth. But in whatever manner the various issues apportion themselves there are certain fundamentals that underlie all pathological research and application. For example, any control method must be viewed not only in relation to the expense of its application and its commensurate return, but also in relation to its social,

economic and political implications. A method suitable for a highly organised plantation system might be quite unworkable under a system of individual or peasant cultivation. A method which might be adopted successfully by an educated community might fail dismally in an ignorant community or, alternatively, succeed in such a community with a trained executive. Methods suitable for single-crop systems of cultivation are often unsuitable for rotation systems. Methods which may be used successfully in pure-line or clone culture may fail in mixed-population culture. Plant introductions, embargoes and quarantines may need to be modified in relation to free-trade or protectionist policies. And, fundamental to all issues, is the purely economic one of the cash return of the crop, perhaps low prices on a bumper crop, high prices on a small crop, world prices, domestic prices and so forth.

Before leaving this aspect of our discussion let me indicate briefly certain issues of plant pathology which seem to me of primary importance to-day, issues upon which research is most urgently needed.

Firstly, the whole congeries of problems concerned with the relation of meteorological, edaphic and nutritional factors to parasitic disease. At Rothamsted Mr Stoughton and myself are commencing the study of physical and nutritional relationships, both in their fundamental aspects and in direct connection with certain diseases of the cotton plant.

Secondly, the physiological-genetic study of parasitic fungi and bacteria. At Rothamsted, Mr Dickinson, Mr Stoughton and myself are working on these problems.

Thirdly, the epidemiology of plant disease, a subject on which we possess very little accurate knowledge.

Fourthly, the nature of the several kinds of susceptibility, tolerance, resistance or immunity to disease. At Rothamsted Miss Glynne is studying certain aspects of these problems in relation to Wart Disease of potatoes.

Fifthly, the field selection or breeding of resistant and immune varieties in relation, on the one hand, to strains of parasitic organisms and, on the other hand, to geographic and climatic areas.

Sixthly, the whole new world of problems included in virus diseases of plants. This complex of troubles surely forms one of the primary controlling factors in the world's agriculture to-day but, considering the importance of these diseases, deplorably little is being done in their study. One of the main reasons is that so few pathologists are really competent to carry out investigations into these difficult and obscure regions, for it is imperative that such work should be done with a meticulous accuracy and impeccable technique such as have rarely been demanded in previous phytopathological studies, and, also, that it should be done with full cognisance of similar researches into virus diseases of animals and man. At Rothamsted the virus disease investigations are being carried out by Dr Henderson Smith.

Seventhly, the possibilities of the cultural control of disease. This is a much neglected but extremely promising field of research which might give immediate practical returns. Of the possibility of the biological control of fungal and bacterial parasites, analogous to the biological control of insect pests, I am not sanguine.

Eighthly, the whole complex of pathological problems connected with transport, storage and marketing. Such researches are almost an untouched field in this country but have a future of tremendous importance.

Ninthly, the physico-chemical basis of methods of plant protection. At Rotham-

sted Dr Tattersfield *et al.* are studying these problems in relation to entomology and parallel researches from the fungal and bacterial side are urgently needed.

Tenthly, the practical value of the several grades of embargo, quarantine, etc., and of legislative action in controlling the dissemination of plant pests.

Lastly, the methods of estimation and statistical analysis of the incidence of disease and the losses from disease.

Of course plant pathology is "so full of a number of things" that one could continue listing problems for some considerable time, but, those that I have just suggested, do seem to me to be of such outstanding importance that any addition to our knowledge would very materially increase our prospects of understanding and controlling plant diseases. It may be noted that certain of these problems might be considered of merely theoretical interest. Well! plant pathology has been such a mushroom growth, and so empirical has been its development, that it has had no time to think philosophically or consider its theoretical foundations. Speaking generally and with, as it were, a long distance point of view, I am of opinion that the greatest need of our science to-day is theory and that with an advance in our philosophy will come a real advance in our practice. It is thus that I find myself, a little to my surprise, holding orthodox views as to the need for more fundamental research. The only proviso I would make is that some of the energy devoted to this end should be directed towards synthesis and not, as at present, wholly towards analysis.

So far I have dealt only with the first portion of my subject, the "research aspects," and I now wish to pass to the second portion, the "applied aspects."

Applied Aspects.

Of the vast amount of data, or of knowledge, acquired during passing years by scientific investigation the greater part that reaches publication stage is printed with all due ceremony in some technical journal and so quietly laid to rest. Occasionally the corpse is disinterred and its bones examined but the second burial is usually quite final. Now a fraction of this research has potential practical value but it is rarely or never carried beyond the laboratory stage and so this value is usually lost. The questions I wish to consider with you are, firstly, how the knowledge that we possess written in technical jargon or locked away in scientific journals can be popularised and disseminated and, secondly, how potentially practical researches can be carried forward to a stage of successful application. I shall discuss these aspects in turn under the headings "popularisation of knowledge" and "application of knowledge."

Popularisation of Knowledge.

There are perhaps three main avenues by which knowledge concerning plant disease in its several aspects may be spread among a rural population.

In the first place is what may be called the teaching avenue which commences with the elementary schools, more especially, perhaps, the rural schools. I think we are all orthodox in our demands for far more biological teaching in schools but, where I should perhaps go beyond many, is in my insistence on the fact that, even in school-teaching, disease and death should be regarded as just as much a part of the normal life-cycle of animals and plants as are birth and health. The two form the complete circle and, to leave out one-half, is to falsify every issue for each only has meaning in values of the other. More biological teaching and, what is equally important, sounder biological teaching, in the schools would go far to produce a rural com-

munity with a more understanding mind concerning health and disease, life and death, not only in plants but in animals and man. More advanced and formal teaching concerning plant diseases is given to a moiety of future cultivators in agricultural high schools and colleges, horticultural institutions and so forth. In all of these, problems of disease and death are usually cut off from normal plant functioning as though they were something not mentioned in polite botanical circles. This, I think, is a mistake. An extraneous teaching avenue, which one almost hesitates to mention, is wireless broadcasting, but so many receiving sets are now spread widely over the countryside in all lands, that it is quite obvious that this avenue might become one of the most important not only for general instruction relating to plant disease but of very direct and urgent use in the face of sudden outbreaks or epidemics of disease.

One of the main avenues of popularisation leading to the adult rural community is the formal lecture system—there are lectures organised by government departments or subsidiary services, lectures by educational and research institutions, lectures by growers' organisations of all kinds, lectures *ad hoc*, lectures almost *ad nauseum*. The value to the lecturer, especially if he be a right-wing man, in giving him contact with the practical farmer and grower is undoubted, but, after a considerable experience of lecturing, I am becoming sceptical of much value, save in the most general sense, accruing to the practical man.

Infinitely more important than formal lectures, to my way of thinking, are actual demonstrations, field trials and experiments, if possible carried out locally in the districts or conducted more centrally by agricultural colleges or research stations, and actual demonstrations of laboratory research in progress. Intimate contact of practical man and research man by visits of farmers, horticulturists, and foresters to educational and research centres and much more visiting in the converse direction, would induce a far greater appreciation of scientific research work and go a longer way to the encouragement of an educated adult rural community than any amount of sporadic lecturing. The only essential is that any demonstration of research should not be a perfunctory showing by an unwilling and bored junior, but should partake of the nature of an actual educational experiment by an enthusiastic and skilled demonstrator who can meet the practical man half-way.

A second primary avenue of popularisation of scientific knowledge may, perhaps, be termed the official channel. By this I mean the central official pathological laboratories and field services, the advisory and inspectorate organisations, the smaller local organisations and extension services, the official channels in growers' organisations and so forth. All of these carry on valuable activities and, mostly in respect of particular and local problems, do transmit to a minority audience knowledge concerning plant disease. Personally I do not think too much importance can be attributed to the growers' organisations and, I feel strongly, that their potentialities for the spread of knowledge have not been sufficiently recognised or developed.

A third main avenue of popularisation of knowledge is printed matter. Here are included notices of legislative enactments regarding disease, the excellent leaflets on specific plant diseases issued by the Ministry of Agriculture and the agricultural colleges, the official journal of the Ministry and various year-books. Other countries have developed such official publication to a greater or a less extent. In the United States of America, for example, this avenue is tremendously developed; many of us who have to read the publications sometimes feel that "overdeveloped" might be a truer word. In this country a recent and noteworthy attempt to give the practical man an idea of what is happening in research laboratories financed by the Ministry

of Agriculture is the volume by Wilkins entitled *Research and the Land*. Records of scientific activity are also attempted by the Royal Agricultural and Royal Horticultural Societies and of more popular nature are such publications as the *Fruit Grower*, *Farm and Field*, the *Gardeners' Chronicle*, etc. A further channel of dissemination which is becoming increasingly important is trade advertisement and propaganda.

Surveying the issues broadly it is very difficult to estimate the value of these different avenues of popularisation. I imagine that no one questions the immense importance of the mental perspective of the rural community towards crop growth, determined initially in the rural schools. After a considerable experience of lecturing to all sorts and conditions of audience I am inclined to think that, as a means of conveying data or knowledge, incidental lecturing to farmers and growers is of comparatively little value, save, as I have already indicated, to the lecturer. The rare man who can strike the imagination of his hearers and arouse enthusiasm in them to take up special questions as a personal interest is, of course, in a different category. One of the most painfully outstanding things in modern science, however, is the rarity of such men. Organised courses under such conditions as those obtaining in the Workers' Educational Association would also, I think, need to be regarded differently and if the rural community could be invaded by a W.E.A. having biological interests this channel might become of extreme value. My experience and opinion regarding the value of printed matter is that, commonly, it is astonishingly less than might have been expected, for the practical man seems often to find it very difficult to translate the published word into terms of personal experience and field practice.

So far as my personal experience goes, by far the best avenue of popularisation is by quite informal discussion with growers, and, above all things, by practical demonstrations where the grower can see things for himself, in the flesh as it were, and make his own judgments in the light of his own knowledge and experience. I feel that I cannot advocate too strongly the value of such intimate and informal contact between the research man and the practical man, and one of the best ways to bring this about seems to me to multiply opportunities of contact by field and laboratory demonstrations, informal discussions and any other way in which the field is brought to the laboratory or the laboratory to the field. I think if energies were directed to this end by the organisations existing on both sides, the spread of scientific knowledge among the adult rural community, and, what is equally important, the spread of practical wisdom among the adult scientific community, would increase rapidly, and we should advance toward that sympathetic and understanding liaison of research and practice which is so urgently to be desired.

Let me now pass to what is the final matter I wish to consider with you, namely, the actual mechanisms of liaison and application.

Application of Knowledge.

The channels by which new processes or new products may be conveyed to the practical man, so that they become an integral part of his practice, are very numerous and varied.

Firstly, there is what may be termed the official channel. In the majority of countries there is a more or less official chain of universities, research stations, government pathological services both central and local, inspectorate and advisory services, extension officials and so forth. Implicit in this organisation is, I suppose, the idea that research coming from the right wing which might have a practical outcome is

taken up by the more left wing services and worked out in its practical or field applications, ultimately finding its way *via* the inspectorate, advisory or extension services into actual practice.

Secondly, there is the commercial channel. On the one hand, research emanating from "private" laboratories or from any published source may be worked out to a commercial issue by the scientific officers of an interested firm and put on the market *via* commercial channels for private profit. On the other hand, a non-profit-making syndicate might be formed to provide facilities for the practical working out of a scientific discovery, to commercialise the product or process and put it on the market in the interests of the further development of the particular issue. Such, for example, was the procedure adopted in the exploitation of the "Adco" manurial process.

Thirdly, there is what may be termed the Institute method. The scientific staffs of crop stations or other similar institutions, not only carry out applied research, but investigate in their own legitimate interests the practical value of any published research, perhaps modifying or carrying on a more theoretical investigation to a practical issue. Such stations are usually conducted in the interests of one or more special crops and the organised growers not only have direct and often predominant representation upon the governing body of the station, but take a very lively and keen personal interest and pride in the work done. Both by intimate personal contact, demonstrations and publications, results of practical value are made known immediately to the growers who put them into actual practice under the advice and often under the personal supervision of the scientific staff. In many countries there are central institutions more or less comparable to the National Institute of Agricultural Botany at Cambridge, and these take a greater or lesser share in the application of scientific knowledge to field practice. Apart from the Wart Disease of potato trials carried out by the N.I.A.B., no pathological work, so far as I am aware, is done under the aegis of this Institute and there seems ample scope for the extension of the activities of such a foundation into the realm of disease.

Fourthly, is what may be called the extension avenue. Except in so far as extension work is carried out in this country by the Ministry's inspectorate and the advisory services this channel which in Denmark, the United States of America and many other countries is so important and vital, is little developed. It is, of course, an avenue of popularisation as much as application but in the U.S.A. where the Extension services are linked, on the one hand, with the experimental stations, and, on the other hand, with the growers' organisations, it is undoubtedly one of the largest factors in actually getting knowledge applied.

Fifthly, is what may be called for want of a better term, the *ad hoc* mechanism. There are already many committees of public, scientific or practical organisations which have been created specially to look after particular issues. Committees of responsible bodies such as the Ministry of Agriculture, the Forestry Commission, the Royal Agricultural, Horticultural or Arboricultural Societies and so forth might well be created *ad hoc*, on need being shown, for the obtaining of facilities for the carrying on of a laboratory research to a practical end, and for ensuring in any feasible way, that the results were made available for successful adoption in practice.

Lastly, is what may be termed the personal channel. In this case the research man himself carries on his work to the practical stage, and then, by his personal effort, sees it through the avenues of propaganda or other mechanism of publicity and finally puts the process or product upon the market, or in some other way ensures its adoption by the grower or interested party. The man who is best for the pure investi-

gational aspect is rarely the man most suited to propagandist issues or one who shows any great acumen in the commercial exploitation of results. I think many of us must know workers of considerable research ability who are becoming, or have become, lost to science, because willingly or not they are following up their research work into the arena of practice. On the other hand, such a method does tend to maintain stricter accuracy in the actual presentation to interested parties of the facts of the case and, further, keeps alive an atmosphere of single-minded purpose and personal enthusiasm which often leads to success.

Of course in discussing any of these mechanisms of application, and this also applies to avenues of popularisation, the several methods I have indicated do not, in actuality, work independently but form a complex in which one aspect or another becomes increasingly emphasised or predominant. Further, the choice of avenue is often, to a large extent, dictated by the source of the knowledge or applied research. With the increasing tendency of commercial organisations to retain their own scientific officers it is obvious that an increasing amount of research or application, deriving from commercial laboratories, will be marketed for profit by the organisations concerned. Again, the avenue depends considerably upon the type of "goods" to be marketed or distributed. Certain products or processes are marketable whilst others are not; thus it is a simple matter to put on the market a new immune variety, a new spray mixture, a new type of machine and so forth, but a difficult thing to make available for successful adoption a new cultural operation, a new planting time or new hygienic methods in which the active and intelligent cooperation of the grower must be enlisted and which he, personally, may need to carry out without any obvious and immediate return. The mechanism of application thus further depends upon the type of community, whether one of centralised plantations or of peasant cultivation, an educated community, or an ignorant one and so forth. Finally, the question of "politics" may be involved, embargoes, quarantines, import regulations, diseases and pests legislation, etc., but as Mrs Alcock has already considered this aspect I shall not discuss it further.

In the field of "application" as in that of "popularisation" I feel that I cannot emphasise too strongly the value of small "crop" or "cultivation area" stations in which there is the most intimate contact between scientific investigator and practical grower. If I may be forgiven an actual example I would instance the Experimental and Research Station, Cheshunt, where work on tomatoes and cucumbers is carried out. I would state, however, as my considered opinion, supported by every shred of my personal experience, that it is most desirable, indeed almost imperative, that such crop stations should be kept small. If it is found that one small research centre in any area is insufficient for the needs of that area or crop then, the original station should not be increased in size, but a second one should be established. In this country, for example, I do not think any more large central stations are required; if money is available the existing ones might be better staffed and equipped. On the other hand, I do not think we can have too many small unit stations, and I look forward to the day when the agricultural, forestry, and other cultivation or crop areas will each contain a smaller Cheshunt or East Malling. What I would like to see are small, simply but adequately equipped laboratories, with if required mobile adjuncts, containing three or at the most four trained men—a plant pathologist, a crop physiologist, an entomologist and a chemist. These men should be essentially field men with a practical outlook and an intuitive "flair" for the growing and regimented crop plant. Their appointments should be conditional on their spending three or four months of each year, or

one year in three or four, carrying out study or investigation in some University or primary research centre like Rothamsted. Their work should be essentially practical research on local problems; not academic work as so frequently is done now but actual frontal assaults on field problems of disease, a large number of which are susceptible to direct empirical attack in the total absence of theoretically desirable knowledge. Further, they should carry out experiments and demonstrations under controlled and under local commercial conditions. I think that the establishment of such units would ensure not only fruitful research on problems of diseases of plants in the field, glasshouse or plantation, but it would multiply opportunity for extensive popularisation of such knowledge, and give prospect of the successful adoption by the practical man of prophylactic and therapeutic treatments. It would lead directly to the integration of practice and research which is the great desideratum.

If one looks over the whole field in the light of one's own experience, both in this and other countries, one cannot help feeling that there exists a real need to-day for a wide survey, somewhat along the lines I have suggested in this address, of the problems of research and practice in relation to disease in cultivated crops. But such a survey needs a broad and constructive vision, that would transcend vested scientific interests, and a courage that would not hesitate to suggest building here and scrapping there in the interests solely of progress towards plant health. If real advance is to be made, it is essential that all the primary issues of pathological research shall be covered economically and thoroughly by men of sound training, of practical outlook and with direct knowledge of commercial conditions. And, secondly, it is essential that relevant information shall be made available to the practical man in such a way that it shall be adopted, translated into field terms and successfully applied. The greatest need in the control of plant diseases is to integrate research and practice and to bridge the gulf from both sides.

As many, perhaps most in this audience are teachers or senior students of botany, agriculture or plant pathology, I would like to say, in concluding, what to my mind is the most fundamental thing of all. I would plead that in our studies we break away from the arid and sterilising grip of unimaginative empiricism in which our sciences are held to-day, that we abandon the dreary and paralysing formalism of "pure" academic tradition and cloistered scholasticism and, whilst retaining all that has value in "pure" science, mould this science fundamentally and boldly to the needs of the new era and the new human issues. That we go out into the world and seek our inspiration in the reality of the growing plant and largely in the plant grown to satisfy human need, for only so shall we keep in tune with the progress of our times and minister to human welfare. Future knowledge depends largely upon to-day's students and what I feel we need, above all things, is to arouse enthusiasm in our students, to strike their imagination, so that they shall go forward not only with accurate knowledge but with faith and vision, a faith that is deep and a vision that is wide and constructive. We must realise that, although as academic beings, it *is* worth while studying grass for the sake of studying grass yet, as human beings, it is perhaps an even nobler ideal to study grass for the sake of making two blades of grass grow where one only has grown before. And finally we must so teach and so wean our students that they shall have a more "gestalt" perspective and a more "holistic" philosophy, so that their ideology shall be one of relationships, in which the phenomena of health and disease are perceived, not as mere isolated things, but as events in the pattern of life and death. In such case I have little doubt that disease in plants is a matter for human control.

REVIEWS

Cotton and its Production. By W. H. Johnson. Pp. xxvii + 536; 26 maps. London: Macmillan and Co., Ltd., 1926. 25*s.* net.

Cotton. By H. B. Brown. Pp. 517; 139 figs. New York and London: McGraw-Hill Book Co., Ltd. 1927.

Since the publication by the United States Department of Agriculture in 1896 of its *Bulletin* No. 33, "The Cotton Plant, its history, botany, chemistry, culture, enemies and uses," no important treatise covering the same large field has appeared until the nearly simultaneous publication of these two manuals. Although both cover the whole field of cotton in all its aspects, the authors have approached the subject from different angles. In *Cotton and its Production* the outlook is mainly commercial, and the subject is treated geographically. Each of the cotton-growing areas of the world is considered in turn and their particular problems of cotton cultivation and production discussed. The purely botanical aspects of the genus *Gossypium* are dismissed in twelve pages, while cotton breeding is treated of in nine. One of the most interesting chapters is that on cotton growing in India. The area planted annually to cotton in India is only one-third less than the whole of the Cotton Belt of America, but owing to the inferior yields the crop is only one-third as large as the American crop. The average yield in India varies in different years from about 60 lbs. to 100 lbs. of lint per acre but has never exceeded 100 lbs.; the yield in America is at least twice this. While it is realised that this poor yield is due in part to unavoidable factors such as unfavourable climatic and soil conditions in many parts of the country, yet, as Mr Johnson points out, still more is it due to a lack of knowledge, and intelligence to apply knowledge, on the part of the peasant grower. A great deal has been done to improve this state of affairs by the Agricultural Departments, while the Co-operative Credit Societies have enabled the small-holder to obtain the capital he needs for his initial outlay without recourse to that prince of usurers, the native money-lender. How much has been done to improve the yield is seen when it is considered that for the five years before the War, 1909–14, the average yield per acre was 77 lbs. of lint, while for the five years 1920–25 the yield was 90 lbs. of lint per acre.

Of much interest too is the chapter on cotton growing in Australia. In 1920–21 Mr Johnson visited Australia on a special commission to enquire into the possibility of developing the cotton-growing industry, and the substance of his reports is contained in this chapter. A huge area in the continent is suitable for the growing of cotton but the extreme sparseness of the population makes its production on a large scale extremely difficult. The author points out that a farmer with a medium-sized family can do all the work on a cotton farm up to ten acres without outside assistance, the labour required for picking being the factor which fixes this limit. Great efforts are being made to improve the varieties grown and to see that the wholesale mixing of seed that has occurred in the past should cease. The export of Australian cotton has risen from 30 bales in 1919 to over 11,000 bales in 1925.

The chapter on the diseases of the cotton plant is not so good. The sketchiness of the treatment and the somewhat inaccurate statements made indicate only a slight acquaintance with the subject. A "boll rot," said to be due to *Bacillus gossypinus* Stedman, is described as being "commonly met with in the United States and the West Indies," whereas it was shown many years ago that Stedman's green flourescent bacillus was not pathogenic. "Internal Boll Disease" caused by Nowell's Species A, B, C and D (*Nematospora*, *Eremothecium*, and *Spermophthora*) is dismissed in two sentences, despite its great economic importance in the West Indies. Insect pests are treated at greater length and in more detail.

Coming to Prof. Brown's volume we find the subject treated, as we should expect with a geneticist as author, far more from the botanical standpoint. The first seven chapters are concerned entirely with the botany of the cotton plant, its species, varieties, morphology, and reproduction. It is surprising that, considering the immense economic importance of the crop, so little research has been done on the physiology of the cotton plant. The monumental work of W. L. Balls in Egypt is almost the sole source of our knowledge. What data there are, however, are very ably presented by the author in this volume, and the physiological problems arising are interestingly discussed. Forty-three pages are then devoted to the genetics of the cotton plant and the known facts are excellently reviewed.

Soils, climate, and cultivation receive considerable attention.

Diseases are treated in rather more detail than in *Cotton and its Production*, and the information given is more in accordance with modern views. However, like many others the author accepts the attribution of Wilt Disease to *Neocosmospora vasinfecta* (Atk.) E. F. Smith, although the evidence on which this fungus was stated to be the ascigerous stage of *Fusarium vasinfectum* was more than inconclusive, and is discounted by most authorities on the subject. As the author states in the preface, the information in the book applies chiefly to the Upland cotton area of the American Cotton Belt, and this accounts for the extent to which "wilt disease" and "anthracnose," the most serious and widespread diseases in this area are discussed, while "Internal Boll Disease" does not even receive mention.

The commercial aspects are interestingly and clearly handled in both volumes, though perhaps more detailed and carefully illustrated accounts of the processes involved in spinning and weaving would enhance the value. Together the two books constitute a most comprehensive treatment of all aspects of cotton and its production.

The bibliographies are more complete in Prof. Brown's volume, the specific citations in Mr Johnson's work being confined to books only. The style of both volumes is excellent and maintains the standard set by these publishers. The maps in *Cotton and its Production* are particularly clear and valuable, although the book as a whole would have been improved by illustrations. *Cotton* is typical of the very high standard of the McGraw-Hill publications.

R. H. STOUGHTON.

Economic Biology for Students of Social Science. Part I. Harmful and Useful Animals. By PHILIPPA C. ESDAILE. Pp. xv + 175; 150 illustrations. University of London Press, Ltd., 1927. 7*s.* 6*d.* net.

The aim of this book is to present the elementary facts of economic biology from the standpoint of "Household and Social Science." It is an attempt to cover a rather ill-defined field which does not seem to have been catered for by any book of a similar character. Dr Esdaile's efforts aim at giving such information that is most generally useful concerning certain animals and plants which are, or may be, associated with man and the household. The present volume which forms Part I deals with harmful and useful animals, while Part II, it is mentioned in the Preface, constitutes a companion volume which treats of animal and plant products.

Such a work as Herrick's *Household Insects* covers only that branch of the subject as is implied by its title, while Dr Esdaile's book is of a much wider scope although less detailed in its method of treatment. The difficulty in writing a manual of this character lies in the choice of material, since the subject in its present aspect has not so far assumed very definite boundaries. Its authoress has taken a wide viewpoint and included all organisms from Protozoa to Arthropoda wherever they betray any relation to her subject. Vertebrates, it appears, do not come within the scope. Chapter I is concerned with the Protozoa and an account is given of the species of *Entamoeba* found in man, of the malaria Plasmodium and its relation to *Anopheles*, together with some brief remarks on the *Spironema* of syphilis and the causation of that

disease. Chapter II deals with the Porifera and their general structure, together with a list of the economically important species and their special uses to man. Flat worms form the subject of Chapter III and a clear, but brief, account is given of the structure and life-histories of the liver fluke of the sheep and of tapeworms; while certain economically important round worms are dealt with in the next chapter. The Insecta form the subjects of Chapters V to XII and practically all the important species affecting man in person or his stored products, in so far as Britain is concerned, are mentioned. Spiders and economically important mites are dealt with in Chapter XIII and the concluding chapter is devoted to general hygienic measures. The book is also supplied with a glossary of the technical terms used, and an index.

We have little to offer by way of criticism, but in dealing with the Hymenoptera, reference might well have been made to ants which can be troublesome invaders of the household. Under the Diptera we miss any mention of the biting housefly *Stomoxys calcitrans* and in the chapter on Coleoptera *Attagenus pellio* would seem to require mention, since it is usually found in houses where its larva attacks furs, skins, etc. These few omissions scarcely detract from the value of the book and attention is directed towards them in the event of a second edition being called for later.

The general impression derived from reading this manual is clarity of expression, accuracy and strict elimination of wordiness. It is, in fact, rigidly confined to essentials, and we may say that the task is well done. Preventive or remedial measures are given wherever desirable and those advocated are up to date and eminently practical. The book is well adapted as an elementary manual and it should meet with a ready demand among the type of reader it is intended to cater for. It is clearly printed in good type and the illustrations are adequate.

A. D. IMMS.

Genetics in Relation to Agriculture. By E. B. Babcock and R. E. Clausen. 2nd ed. Pp. xiv + 673. McGraw-Hill Book Co. 1927. 25*s*. net.

Few aspects of science have shown so remarkable a development as modern genetics, which beginning almost *de novo* a quarter of a century ago, has acquired a mass of exact data and fundamental theory that will bear comparison with those of any other scientific discipline. This, in part, is due to the curiously post-dated birth of genetics and the correlated fact that a great amount of anatomical, cytological and other exact information and practical breeding experience were available which could be incorporated immediately as a broad and stable foundation for the new development. In the quite early years certain fruitful lines of investigation began to crystallise out: on the one hand, the study of the mechanism of Mendelian heredity and the relation of the gene to character effect and, on the other hand, the study of pure-line analysis and the more empirical splitting and synthesis of the phenotype. The genetic research of the last 25 years has been almost entirely an advance along these lines and the main congeries of obvious problems have been more or less explored, the greater number of geneticists being now engaged in filling in details or showing the application of already formulated theory to further examples. Broadly speaking, this, the first period of genetic development has come to an end and the science is in the throes of a re-birth. The atomistic ideology of genetics is in process of rapid change, a dynamic philosophy arising on the foundation of the static philosophy of the last quarter of a century. It is a transition that is clear not only in the more enclosed field of genetics but in the whole biological and psychological landscapes, mechanistic philosophies sublimating into hormic or dynamic philosophies. The atomistic ideology of genetics from 1900–25 might almost be regarded as a necessary pre-requisite for the emergent evolution of the science to a functional plane, a plane on which genetic phenomena are perceived as events rather than things. Of the one school of philosophy it might be said that the teachers are Johannsen and Morgan, of the other school, Bateson and Goldschmidt, with Baur as a bridge between the two schools and Lotsy as *Advocatus Diaboli* in general. Such work as that of Goldschmidt (see for example his recently published *Physiologische Theorie der*

Vererbung, 1927) or particulate researches such as that of Plunkett, are not merely an additional new line of study but an entirely new viewpoint and a new plane of exploration. They are the foundation stones of a developmental genetics and a dynamic philosophy as against the older mechanistic genetics and static philosophy. There would seem little room for doubt that the science of physiological genetics opening before us will entirely re-orientate genetic theory and philosophy.

It is desirable that, at the close of a period, stock should be taken and the general position reviewed so that a vantage ground may be selected for further endeavour. This has been happening in genetics and the cognate disciplines. On the cytological side volumes have appeared by Cowdray (edit), Wilson and Sharp. In genetics itself are the monographic volumes by Fruwirth and the series edited by Baur and by Lotsy and Kooimanns. Of single treatises covering the entire field or on one or another aspect of genetics are the volumes by Crew, Rice, Hayes and Garber, Shull, Sinnott and Dunn, Babcock and Clausen, Jones, Johannsen, Baur, Castle, Walter, Morgan and others. All these have been published during the last two or three years and to a greater or less extent review the position to date. Certain of these volumes are second editions and a comparison of two editions is always interesting for it enables one to measure the progress that has been made in a specified period. For example the time elapsing between the second and third editions of Wilson's *The Cell* corresponds with the life of modern genetics, 1900–25, and a comparison of the two editions gives an extraordinarily clear picture of the development of cytogenetics. If one compares the 1913 and 1926 editions of Johannsen's treatise one, similarly, obtains a view of progress in pure-line theory and practice. Perhaps the best picture of the advances in general genetics is obtainable from the several editions of Baur's volume, or from the three editions of Castle's treatise although this gives a more personal point of view.

An excellent idea of the general advance in genetic development made during the last decade is obtained by a comparison of the first edition of the work by Babcock and Clausen published in 1918 and the second edition which has just appeared. In 1918, for example, the fundamental importance of the chromosomes in genetic theory although strongly indicated might still be regarded as a moot point, whereas to-day, the value of cytogenetic research is no longer in question. The applied value of genetic research in animal and plant breeding was, in 1918, still largely a matter of hope and promise, whereas to-day much of that promise is not only well on its way to fulfilment but certain issues of primary horticultural or agricultural importance have been solved outright. It is interesting to contrast the development of genetics during this period and its outlook to-day with those of, for example plant pathology, one of the few aspects of biology which has shown an equally rapid growth. In plant pathology the development has been almost entirely empirical and the singular lack of fundamental research and theory has given rise to an unstable, because unbalanced, structure. In genetics, on the other hand, theory has advanced naturally and logically in the van of practical application, and perhaps nothing characterises the close of this youthful period of genetic development so much as the broad advance made in fundamental research and the stable balanced nature of the resultant growth.

The genetic progress during the period 1918–27 is well reflected in the difference between the two editions of Babcock and Clausen's volume. Both are divided into three parts—I. Fundamentals, II. Plant Breeding, and III. Animal Breeding, but whereas in the second edition it has been found possible to reduce Part III from 172 pages to 134 pages and Part II from 156 pages to 148 pages, the same process of condensation applied to Part I has necessitated an increase in number of pages from 286 to 330.

This fundamental advance is, of course, largely due to the work of Morgan and his collaborators and the first portion of the volume is principally based on the researches of the Columbia school to which it forms an excellent and simple introduction. The only broad criticism one would make of Part I is that it is perhaps too strongly coloured by the researches of the authors' compatriots—Morgan *et al.*, East, Emerson, Blakeslee, Jones, Castle and others and that not sufficient attention has been given to the often divergent views of such European investigators as Bateson,

Baur, Lotsy, Claussen, Turessen, Nilsson and so forth. To take, for example, one issue only, that of sex, with its ramifying implications, the fundamental and revolutionary investigations of Goldschmidt, although referred to in the bibliography, are almost passed over in the text. In detail there are many points of interpretation in the authors' treatment of "Fundamentals" with which one finds it somewhat difficult to agree, but this is only to be expected in so new and rapidly developing a science as genetics. One rather more general issue which underlies the whole treatment of this first part may be noted. The authors have re-classified the phenomena of variation into I. "Developmental variation," II. "Mendelian variation," and III. "Mutation." The first category aligns with the older term "modification"; the second, in part with the older term "combination" but excludes the expression of aberrant or multiple chromosome re-arrangements which along with qualitative changes and all changes of unknown causation are relegated to the third category of "mutation." This last term thus connotes the expression of both qualitative and quantitative changes in germinal elements and is, as the authors state a "catchall" term. This new classification of variation is neither logical or particularly helpful to clear and precise thinking, and it is a pity that in a volume which is obviously destined to become a widely accepted and standard text some more logical categorisation such, for example, as that suggested by Baur in his original treatise ("Einführung in die experimentelle Vererbungslehre") or elaborated in detail more recently by Bridges should not have been adopted.

Part II deals with plant breeding and is an excellent and concise introduction to an extraordinarily wide and diffuse subject. Even Fruwirth's five volumes only partially cover this field and in a book of the present size a preliminary reconnaissance only can be made. The note running through this portion—the urgent need for the most intimate cooperation between practical grower and genetical investigator—is one which cannot be too strongly emphasised.

Part III is concerned with the application of genetics to animal breeding and is a simple and straightforward introduction to what has already been accomplished and of the genetic facts and implications which underlie the occupation of the practical breeder. In a chapter on "acquired characters" much of the diffuse unsatisfactory work in this field is dealt with in an admirably critical way, but one would have liked to see some reference made to the genetic implications of such work of, for example, that of Tornier. One of the most interesting chapters is that dealing with the promising and immensely important subject of animal hybridisation.

The "list of literature" runs to 35 pages as against 26 in the first edition but a number of these items are not referred to in the work, and one finds it a little difficult to understand the inclusion of many of these references, when other more important ones are omitted. No references are actually cited in the text and those at the ends of the chapters, a new feature of this edition, might in many cases have been omitted as they are merely to elementary text-books. The glossary and synoptic contents are absent from this second edition; the text-figures have been reduced from 239 to 203, many of which are new, and the coloured plates have been reduced from five to four of which three are new.

Taking it all in all, one may question, whether the new edition is quite as good a treatise on *Genetics in Relation to Agriculture* in 1927 as was the first edition on the same subject in 1918—certainly it is not as readable, but that is probably due to the difficulty of condensing so enormously expanded a mass of data into the same compass, 673 pages as against 675. In any case the book stands quite alone in its particular field and not only geneticists and agriculturists but all biologists owe a debt of gratitude to the authors for carrying out successfully so difficult and onerous a task.

WILLIAM B. BRIERLEY.

CAMBRIDGE: PRINTED BY W. LEWIS, M.A., AT THE UNIVERSITY PRESS